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PARENTAL STRATEGIES OF THE FERAL INDIAN PEAHEN *PAVO CRISTATUS*

THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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DEPARTMENT OF BIOLOGY, OPEN UNIVERSITY

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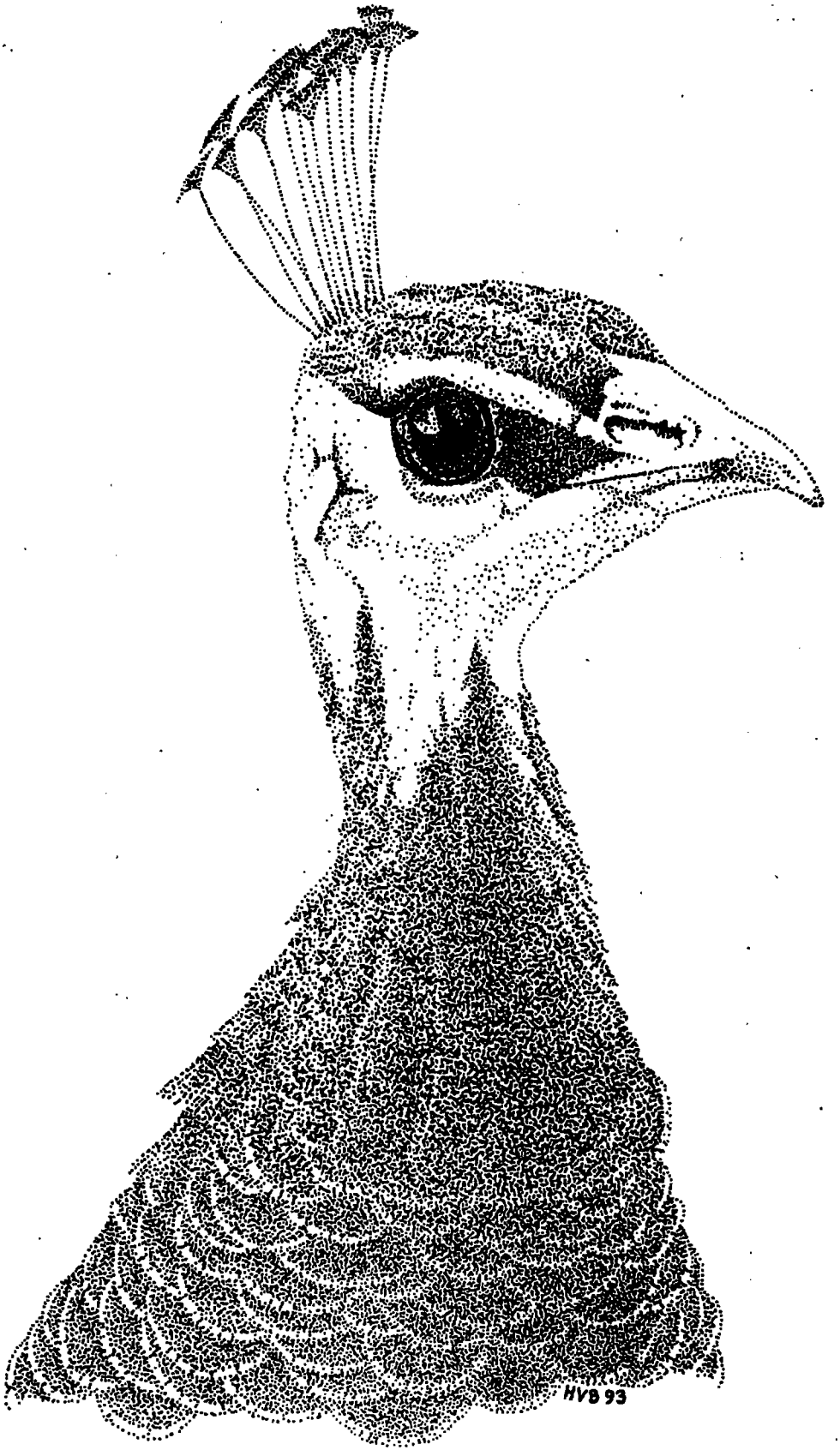

"Female B29"

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ABSTRACT

The Indian peafowl is a large, polygynously breeding species in which the female is entirely responsible for care of the precocial young. Parental expenditure was investigated in peahens throughout incubation and fledging, using both material and behavioural measures of expenditure. The scope of the study was extremely broad, but four main questions were addressed (see below). In addition, the effects of several potentially confounding physiological and environmental variables were considered.

Is parental expenditure related to the residual reproductive value of the parent, or to the costs of expenditure for parental fitness? There is no evidence that peahens vary their expenditure in relation to their own age, and hence residual reproductive value. Female weight also has little influence on investment, except as a constraining factor on the more demanding forms of care, such as brood defence and egg production.

Is parental expenditure related to the reproductive value of the offspring, or to the benefits of expenditure for offspring fitness? Offspring reproductive value is predicted to increase and renesting potential to decrease over the season, but behavioural measures of expenditure do not vary predictably over time. All these measures decline with chick age, suggesting that investment is adjusted to chick vulnerability rather than reproductive value.

Does parental expenditure vary with clutch/brood size in accordance with the predictions for shared and unshared parental investment? Vigilance increases with clutch size but not with brood size, thus supporting the hypothesis that it is an unshared form of anti-predator behaviour (Lazarus & Inglis 1986), for the case that predators typically take an entire clutch but only single chicks. However, brood defence increases with brood size; females may perceive me as a threat to the entire brood, so that defence is shared rather than unshared. More detailed examination indicates that some measures may shift from shared towards unshared investment (or *vice versa*) with chick age.

Is brood amalgamation an adaptive strategy? Observations and playback experiments suggest that both nest parasitism and gang-brooding can be adaptive strategies, whereas dump nesting and adoption may result from particular constraints.

In summary, parental expenditure in the peahen appears to be determined primarily by its benefit for her offspring and its costs to herself, rather than by the reproductive value of either party. Observations generally support the predictions for shared and unshared investment. Brood amalgamation is common, and can be adaptive in some circumstances.

CHAPTER ONE
GENERAL INTRODUCTION

1.1 Aims and approaches

The aim of the study described here is to investigate the nature of parental investment in the Indian peafowl - a polygamous, ground-nesting bird with precocial young. The subject of sexual selection and female choice in this highly sexually dimorphic species has received much attention in recent years (*e.g.* Rands *et al.* 1984; Ridley *et al.* 1984; Petrie *et al.* 1991, 1992), but this study concentrates on reproductive effort during the post-mating period when hens are investing in offspring. Chapter One describes the natural history of peafowl, both in India and in the feral population studied at Whipsnade, and introduces the theory of parental investment that will be used in subsequent chapters.

The general methods used in the project are outlined in Chapter Two, while Chapter Three discusses parental investment in nesting. Egg size and clutch size are used as measures of investment, and behavioural comparisons are drawn between hens by means of time budgets. Particular attention is paid to vigilance levels. An attempt is made to relate the level of parental care to the reproductive values of both females and clutches; as discussed in Section 1.2.2 quantification of reproductive value is often impracticable, especially in field studies, but I believe that measures of the age and size of eggs, clutches and hens (where known) can provide some indication of relative reproductive value. Chapter Three also discusses the phenomena of dump-nesting and intraspecific nest parasitism, and the interaction between incubating females and other individuals.

Chapters Four and Five are concerned with parental care after the offspring have hatched; in common with Chapter Three, behavioural measures are used to determine the relationship between parental investment and brood reproductive value. Chapter Four concentrates on investment in terms of brood defence, while time budgets are once again analysed in Chapter Five.

The care of unrelated offspring is an apparently maladaptive strategy, but has been widely observed among the peafowl at Whipsnade. Chapter Six presents several hypotheses to account for the phenomenon of post-hatch brood amalgamation, and these are tested using playbacks of chick calls to investigate kin recognition and female susceptibility to adoption. Chapter Eight is the final discussion chapter, and draws together the results and conclusions of the rest of the thesis, with suggestions for future research following on from this study.

1.2 Natural History of the Indian Peafowl, *Pavo cristatus* [Linnaeus 1844]

1.2.1 History and origins

The spectacular plumage and flamboyant display of the Indian peacock have made it one of the most familiar birds over the centuries, renowned far beyond the bounds of its native range. It is indigenous to India and Sri Lanka, but man's fascination with this colourful bird means that nowadays it can be found in most tropical and temperate regions of the world.

The history of the species goes back many centuries; peafowl are mentioned even in the Bible (1 Kings x, 22; 2 Chron. ix, 21), and they have always played an important role in legends and folklore (Thaker 1963; Bergmann 1980; Ali & Ripley 1983; Kirkham 1991). According to ancient Greek mythology, the eyes on the peacock's train were taken by Hera from the giant Argus while he slept; but in Western European legend the eyes represent the seven deadly sins, and the peacock is the bringer of ill fortune (Ridley 1981).

Eastern tradition regards the bird much more favourably. In Japan, the god Buddha is sometimes depicted riding on the back of a peacock (Bergmann 1980); similarly in Hindu mythology, the peacock is considered sacred "as the vehicle of the god Kartikeya, the son of Lord Shiva and his consort Parvarti, and a brother of elephant-headed Ganesha" (Ali & Ripley 1983). Since 1963 the species has been protected as the national bird of India (Thaker 1963; Mukherjee 1979).

Peacocks were first brought into Europe by Alexander the Great, who upon seeing them in the wild was so struck by their beauty that he introduced a severe penalty for anyone who

harmed them (Goldsmith 1774; Thaker 1963). Not everyone has been so enamoured of its beauty that they could overlook its other character faults: according to Goldsmith (1774), "the peacock...is said to have the plumage of an angel, the voice of a devil, and the guts of a thief...the horrid scream of its voice serves to abate the pleasure we find from viewing it: and still more its insatiable gluttony, and spirit of depredation, make it one of the most noxious domestics that man has taken under his protection". The Romans however bred them not only for their visual attributes, but also as a delicacy for the tables of the wealthy - although Goldsmith (1774) describes them as being "very indifferent eating".

By the fourteenth century, the peacock had reached as far as England, and has since become a familiar sight in parks, zoos and the gardens of stately homes. They appear to tolerate the colder climate well, and differ little morphologically from their wild relatives, although Sharma (1978) and Bergmann (1980) describe the wild Indian peacock as having longer tarsi than the domestic variety. Although never completely independent of humans, a number of feral populations have established themselves in Britain, and one such semi-wild population is at Whipsnade Wild Animal Kingdom in Bedfordshire (see Section 1.1.3).

1.2.2 Ecology and reproduction

Description of the species

Peafowl are the largest of the Phasianidae, and in common with most pheasants they are extremely sexually dimorphic (Delacour 1977), with the male possessing a highly-specialised ornamental plumage. Two species are recognised: the Indian or Blue Peafowl *Pavo cristatus* [Linnaeus 1758], and the Green Peafowl *Pavo muticus* [Linnaeus 1766], of which there are three subspecies (Bergmann 1980). A closely related genus, *Afropavo*, was discovered in Africa in 1936, but in appearance it bears little resemblance to *Pavo* spp. There are no currently recognised subspecies of *P. cristatus*, although the Black-winged mutant form *P.c.* mut. *nigripennis* [Sclater 1866] has occasionally been described as a separate species (*e.g.* Thaker 1963). Albinism is frequent, and has given rise to two other well-established breeds of *P. cristatus*: the White and the Pied (Baker 1930; Delacour 1977).

Figure 1.1 shows adult male and female Indian peafowl. Unlike the Green peafowl, whose conservation status is considered "vulnerable" by ICBP (King 1981), this species is fairly common both in the wild and in captivity. The male peafowl can be recognised easily by its large size, iridescent colours, erect crest and striking display, and by its loud, distinctive call which can carry several kilometres. The peahen is also crested, but is generally smaller, with a much duller brown plumage and no elongated tail coverts.

The male *P. c. nigripennis* differs little from the Indian, or Blue, peacock, apart from having (as its name suggests) black wings, shoulders and thighs, instead of the barred buff-and-black of the normal Blue. Black-winged females however are much lighter than *cristatus*, having a creamy white plumage with black edges to many of the feathers, and a rufous crest and upper neck. Immatures resemble the female, but first year males are more heavily marked with black (Baker 1930; Delacour 1977; Bergmann 1980).

Both males and females of the White variety are pure white throughout their lives, but unlike other albino forms their eyes are grey rather than red (de Clinchamp 1982). The Pied peafowl has patches of white feathers replacing the normal colours here and there (Delacour 1977), and its occurrence appears to depend on there being a White individual at some point in its ancestry (Bergmann 1980).

All four varieties of *P. cristatus* breed true, and can freely interbreed to produce fertile offspring, with slight variations in plumage. With respect to their ecology and behaviour, there appear to be few major differences between the various breeds. In all varieties, both sexes moult after the breeding season, and moulting takes around two months (Sharma 1974). Feather regrowth begins two or three months subsequently, but is extremely slow (Sharma 1974; Bergmann 1980), and the male's train does not reach full size until the following mating season.

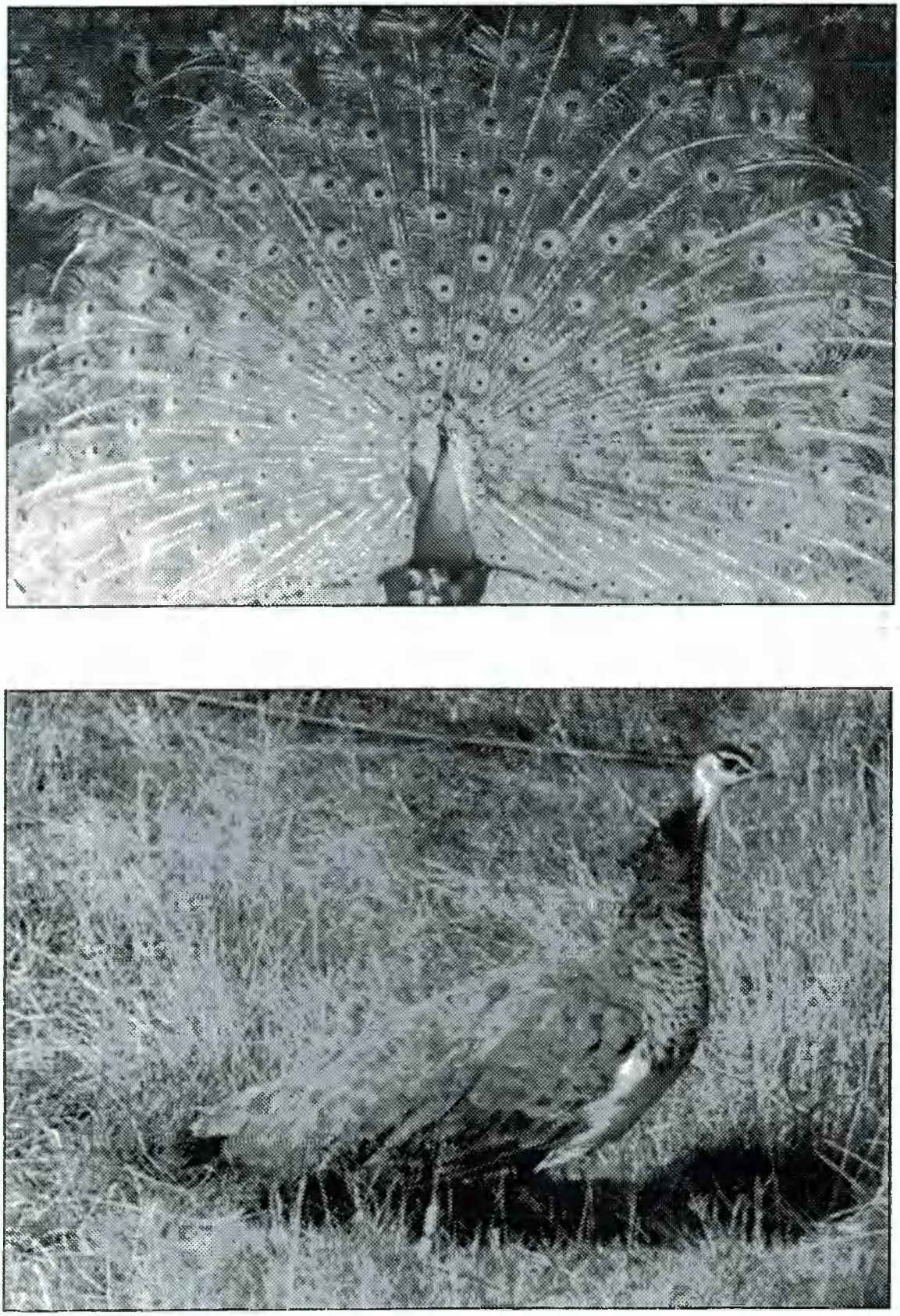

Plate 1.1. Male and female Indian peafowl *Pavo cristatus*.

Habitat and ecology

Peafowl are indigenous to the lowlands (usually below 2000 feet) of India and Sri Lanka, but they have been reported up to 6000 feet in some parts of Southern India (Delacour 1977; Ali & Ripley 1983; Johnsgard 1986). They have a widespread but patchy distribution in a variety of habitats, but populations can be found in most forested areas over the Indian subcontinent (Johnsingh & Murali 1978; Ali & Ripley 1983). Ridley (1981, 1983) proposed a qualitative hypothesis in which peafowl may have evolved from pheasants that inhabited dense rainforest, singly or in pairs. He suggests that as they adapted to more open and patchy habitats, peafowl became gregarious, probably because of the advantages gained from increased vigilance, or better foraging efficiency.

Peafowl are now found in a wide variety of habitats, but their main requirement appears to be the availability of water (Johnsingh & Murali 1978), although Sharma (1972) believes peace and isolation to be just as important as water to the nesting hen. The preferred environment includes tall trees to roost in (Plate 1.2), dense bushes with open areas for breeding, and the availability of adequate nest sites and feeding grounds (Bergmann 1980; Johnsgard 1986). They can be locally abundant, for example around villages and cultivated areas or where they are protected on religious or sentimental grounds (Baker 1930; Bergmann 1980), but in some areas they are persecuted for "peacock oil" which is of supposedly medicinal value (Johnsingh & Murali 1978). Natural enemies of adult peafowl include jackals and dholes (M. Petrie, pers. comm.) and the larger members of the cat family such as the tiger and leopard (Bergmann 1980; Junghuhn, cited in Beekman 1988). Eggs and peachicks can suffer extremely high mortality. Their main predators are stray dogs, birds of prey, mongoose, jungle cats, and local collectors who use the eggs in aphrodisiacs (Baker 1930; Sharma 1972).

Although predominantly a primary consumer, the peafowl is fairly omnivorous, taking seeds, fruits, shoots, insects and small reptiles (Dilger & Wallen 1966; Johnsgard 1986). Junghuhn (cited in Beekman 1988), writes of it also scavenging corpses of dead animals for worms, and according to Goldsmith (1774): "as it is a very proud and fickle bird, there is scarcely any food that it will not at some time covet and pursue".

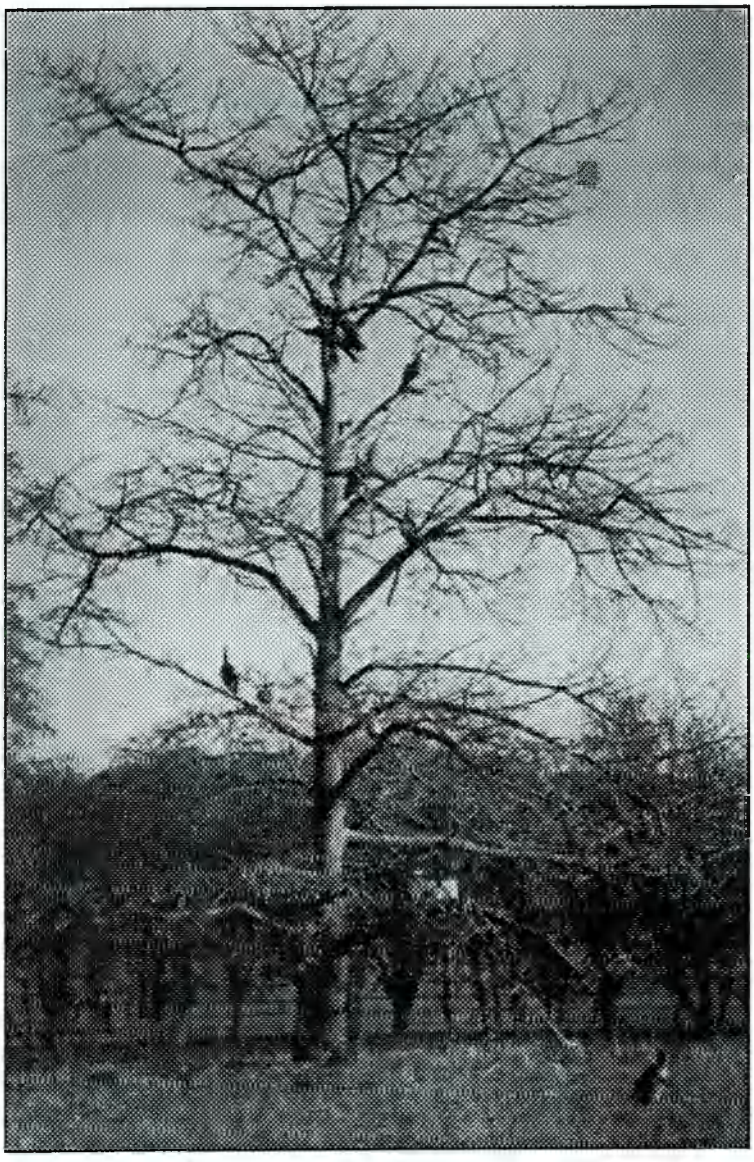

Plate 1.2. Traditional roost site: peafowl going up to roost in tall tree, one winter evening.

Social behaviour

The social system of *P. cristatus* varies according to the time of year. After the breeding season, peafowl have been variously described as moving in mixed flocks (Oates 1898; Delacour 1977; Ridley *et al.* 1984), or in segregated groups of adult males, and females with juveniles (Schaller 1964; Ali & Ripley 1983; Beasley 1986; Johnsgard 1986), while Sharma (1969, 1978) writes of loose, not organised, flocks.

Their gregarious nature means that peafowl spend most of their time roosting, foraging and resting with other individuals. Sharma (1978) reported the sex ratio of his study population in Jodhpur to be 170-210 males:100 females, but Johnsingh & Murali (1978) found an

inverse relationship, with only 47 males:100 females. Adult peafowl roost at night in tall trees, often in large numbers, but tend to spend daylight hours in smaller groups (Bergmann 1980; Navatheekannan 1984). The roost trees are traditional sites to which the birds return every night, so home ranges are generally small (Johnsingh & Murali 1978; Johnsgard 1986).

Groups of peafowl forage and drink in the early morning and late afternoon, and spend the heat of the day resting and preening in the shade (Navatheekannan 1984). Individuals have often been observed "allo-grooming" during this period, pecking small parasites from each other's heads (Sharma 1972, 1978; Hillgarth 1984; Ridley *et al.* 1984), and Sharma (1969, 1978) also described juveniles engaging in the unusual behaviour of "group play".

These daily routines were studied by Navatheekannan (1984). The activity rhythms of many birds and small mammals are mainly regulated by the light:dark cycle, although other factors such as temperature or social cues may also play a part (Broom 1981). Navatheekannan found that the daily emergence of peafowl populations was related to photoperiod, with the frequency of birds flying from the roost forming a bell-shaped curve over a period of about an hour at sunrise. In the evening, the movement of peafowl up to the roost was much more closely related to the time of sunset, with the effect that the whole group was going to roost *en masse*. Temperature had no effect on the time of emergence or roosting, but social cues were apparently important in the evening, when there was a significantly higher level of calling.

Communication is very important in a social species such as the peafowl, and their distinctive calls have been described by a number of authors (for a description of 11 categories of calls, see Johnsingh & Murali 1978). The male has two main types of calls: a loud, harsh "May-awe", particularly common during the mating season, and a series of short gasping shrieks "ká-ãn...ká-ãn" - likened to "something between the screams of an hysterical old woman and the bray of a donkey" (Ali & Ripley 1983). The female generally makes few calls except when alarmed, or during the breeding season. A peahen leading her chicks gives a loud guttural "kok-kok", repeated intermittently with neck feathers fluffed out like a bottle brush (Delacour 1977; Johnsingh & Murali 1978; Ali & Ripley 1983). Other

calls include deep "honks" and "honk-caws", made predominantly when the female leaves her nest or when alarmed (pers. obs.).

Mating pattern

There is some disagreement within the literature over the type of mating pattern in operation during the breeding season, although all sources agree that the species is polygynous (*i.e.* individual males copulating with several females) or polygynandrous (*i.e.* both males and females mating with more than one partner). This pattern has commonly been described as "harem-defence polygyny", in which a male is attended by a harem of up to five females (*e.g.* Shaller 1964; Johnsingh & Murali 1978; Ridley 1981; Ali & Ripley 1983; Johnsgard 1986). Sharma (1969, 1978), however, saw no evidence that harems exist in the wild, and suggested that a group of several females incidentally near an adult male may have been mistaken for a harem by previous authors.

As early as 1957, Morris wrote: "only in peafowl...has a trend towards social display evolved that is somewhat comparable to the lek display grounds of various grouse, in which several males gather together in close proximity for display and the female may select a single male from the group for mating". This idea however was widely neglected until 1984, when studies of a small semi-feral population in England provided strong evidence for the existence of a lek mating system (Rands *et al.* 1984; Ridley *et al.* 1984). Such peafowl "leks" consist of several adult males clustering together, each defending small contiguous territories. Displaying males within these territories are only a few metres apart and contain no food resources (Rands *et al.* 1984; Petrie *et al.* 1991). Similarly, Hillgarth (1984) described the breeding of wild peafowl in Gujarat: she found that they formed "exploded leks" (similar to traditional leks but with males much further apart) in woodland, but were more clumped in open land.

Current research generally supports the idea that male peacocks form leks, at which hens may mate with their preferred male. This "female choice" appears to be based on the morphological characteristics of the male (in particular the number of eyespots in the train) which may reflect some other aspect of the male's age, status or condition (Rands *et al.*

1984; Manning 1987, 1989; Petrie *et al.* 1991, 1992). After copulation, the peahen is entirely responsible for parental care, and the male contributes nothing to the next generation except gametes.

Breeding behaviour

Throughout India the timing of the breeding season is varied, but is apparently always related to the onset of the wet season (Thaker 1963; Johnsgard 1986). Sharma (1972) states that laying begins only when rainfall has exceeded 30mm, and rainfall in one year affects the subsequent years' breeding performance. The arrival of the monsoon brings both a marked decrease in temperature, which seems to facilitate male display (M. Petrie, pers. comm.), and an increase in the number of insects, which form a major component of the diet of the chicks (A. Musavi, pers. comm.).

In Southern India and areas with showers early in the year, breeding is typically between January and April (Johnsgard 1986). In most parts of India, however, the monsoon arrives around mid-June, so males start to display and defend lek territories from about February, mating begins in May and egg-laying in June (Sharma 1972). The timing is similar in Europe, but the season is not so restricted by the weather and lasts longer than in India: copulations take place between April and July, and nesting from May to August (Bergmann 1980; Ridley *et al.* 1984).

Peahens make very rudimentary ground nests, usually consisting of nothing more than a shallow scrape hidden under thorny bushes such as *Capparis*, *Zizyphus* or *Lantana* spp. (Sharma 1972; Bergmann 1980). Hens rarely add feathers, which can make ground nests conspicuous to predators (Welty & Baptista 1988).

Members of the Phasianidae lay 1-20 eggs, usually 6-12 (Delacour 1977). Estimates of peafowl clutch sizes vary, but they are generally reported to lay between three and eight (usually four to six) creamy-white or buff-coloured eggs (Sharma 1972; Ali & Ripley 1983). More detailed descriptions of eggs and clutches will be given in Chapter Three. Peahens are normally single-clutched, but there is a high level of nest failure and early chick mortality in the wild, and these birds therefore have a high potential for re-nesting (de Clinchamp 1982;

Johnsgard 1986). Delacour (1977) reports that they are capable of laying three or four clutches of decreasing size, if they are not permitted to sit. Eggs are laid in the late afternoon (Sharma 1972; Welty & Baptista 1988). The female starts to incubate when the clutch is complete (or nearly complete), and seldom after the fifth or sixth egg; the precocial chicks therefore hatch synchronously after an incubation period of 28-30 days (Sharma 1972, 1978; Delacour 1977).

During incubation the peahen remains on her nest almost continuously, and will defend an area around it (Sharma 1969). She leaves it to feed briefly twice a day, once between 0800-1000 hours, and again between 1700-1900 hours (Sharma 1972). The nest requires little maintenance, but the female turns the eggs at regular intervals until they start to pip; this mechanism provides an even temperature throughout the nest, and prevents the embryonic membranes from adhering to the shell (Welty & Baptista 1988). The first chicks hatched are brooded by the mother for a day or so at the nest, and then the shells and any unhatched eggs are abandoned as the female leads her brood away (Sharma 1972; Johnsingh & Murali 1978). Sharma (1972) reports that up to 94% of the eggs are fertilised, and therefore eggs are not deserted because they are infertile; he believes that a female will only care for those young born on the first two days because she cannot control more than five nidifugous chicks. Abandoned eggs are thus usually found in clutch sizes of eight or more.

Chick growth and maternal behaviour

Newly hatched chicks are dry and well-developed, and are able to move at only one or two hours old. The hen leads her nidifugous brood to the shelter of dense vegetation, where for the first ten days they remain very close to her (Delacour 1977; Sharma 1972). The chicks stay in loud vocal contact with their mother, and at her alarm call they will scatter and flatten in the grass, where their brown striped plumage provides excellent camouflage (Sharma 1972, 1978).

At 12-15 days the chicks can jump and flutter onto low perches (Rutgers & Norris 1970; Delacour 1977), and are able to fly short distances at three weeks (Sharma 1972). At four weeks old they begin to grow tiny crests, and by two months of age both sexes have the

appearance of small females (Rutgers & Norris 1970; Ali & Ripley 1983). Before long there is a discernible difference between the plumage of the sexes (Bergmann 1980): immature males begin to develop buff-and-black barring on the back and wing coverts, while young females remain a soft brown with a creamy underside, like their mother (Ali & Ripley 1983).

Although the chicks hatch in a precocial state, subsequent growth and development is relatively slow; young birds stay with their mother for at least five or six months, and do not become completely independent until towards the following breeding season (Sharma 1972, 1978; Johnsgard 1986). Chick mortality is very high in early life, resulting in a modal brood size of two (Johnsingh & Murali 1978), but once the young can fly the risk of predation is greatly reduced (Sharma 1972).

As the young become increasingly mobile, the mother takes them to feed out in the open and to roost at night with the adult groups (Johnsingh & Murali 1978). Peahens are often described in the literature as "excellent mothers" (*e.g.* Delacour 1977). Sharma (1978) even writes: "It was noted that peahen often caresses her chicken and occasionally chicken also do so, in affection, to their mother". A female will protect her brood from harsh weather and predators, and teaches her chicks to forage, by pointing out grains, insects and seeds on the ground (Rutgers & Norris 1970; Sharma 1978). Sharma (1972) writes of her chasing away strange chicks who attempt to join her brood, but Johnsingh & Murali (1978) saw no such female aggression towards any other chick or adult. Both hens and chicks have been observed giving a display that resembles the male's sexual display (Delacour 1977; Bergmann 1980; Ali & Ripley 1983). The female may raise her tail and lower her wings in response to a displaying male, or to an enemy; the chicks often display for no such obvious reason, although in the presence of other chicks it may serve as an aggressive signal.

Maturation

Females become sexually mature and able to rear offspring from the age of two, although reproductive success may improve as the hen gets older (Sharma 1972). Johnsingh & Murali (1978) found that 31% of the 134 females at their study site in Tamil Nadu, India, were breeders; these 42 hens produced a total of 80 chicks in 1975. Sharma (1972) reports

the percentage of peahens reproducing each season to be 25-57%, with more hens breeding in fertile than arid regions; however, he found that the number of young fledged per clutch was more than two in the arid regions, but only 0.5 in the fertile areas. He attributes this anomaly to the higher level of predation and human disturbance in the richer, more populated areas. Sharma also suggests reasons for the high percentage of non-breeding females in the population: he states that 20% are too young (*i.e.* less than two years old); 25% are too old (more than seven years old); and 5% are unable to find a suitable nest site.

Unlike the female, the male undergoes delayed maturation and does not develop the full adult plumage until the age of three* (Delacour 1977; Bergmann 1980; Ali & Ripley 1983). Across all species, sexual bimaturism is closely correlated with polygyny; if females prefer to mate with older or larger males, and the development of secondary sexual characters has a cost, it is adaptive for a male to delay maturation until he has a reasonable chance of securing matings (Lack 1954, 1968; Selander 1965; Curio 1983, 1988; Manning 1985). First year males resemble the peahen, but with a slightly bluer neck and breast, compared to the female's green, and more barring on the wing coverts. The plumage of second year males is identical to the adults', but without the long upper tail coverts; these are developed in the third breeding season, and subsequently continue to lengthen for a number of years (Jerdon 1864; Darwin 1871; Manning 1987, 1989). The lifespan of both males and females is given as around 15-20 years (Goldsmith 1774; Manning 1987), although there are unsubstantiated reports of individuals in captivity surviving up to 40 (J. Manning, pers. comm.) or even 96 years old (Beebe 1931).

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* Recent observations of marked birds introduced at Whipsnade suggest that some males show significant upper tail covert development by their second year (M. Petrie, pers. comm.).

1.3 Parental Investment: The Theory

1.3.1 Males, females and parental care

For most sexually reproducing organisms, males and females invest asymmetrically in their gametes: males produce large numbers of small, mobile gametes (sperm) which contain little more than genetic material, whereas females produce fewer gametes (eggs), but they are larger, immobile and well nourished (Bateman 1948; Trivers 1972; McFarland 1981).

Charles Darwin in 1871 was the first to recognise the importance of these differences, and to encompass them in the development of his theory of sexual selection. He defined sexual selection as (1) competition within one sex (usually males) for members of the opposite sex, and (2) differential choice by members of one sex (usually females) for members of the opposite sex. Bateman's (1948) studies of *Drosophila melanogaster* provided empirical support for Darwin's argument, concluding that females produce far fewer gametes than males, and there is consequently competition between male gametes for female gametes; although his results have not always been accepted as conclusive evidence of non-random mating (*e.g.* Sutherland 1985).

Darwin's concept of sexual selection predicts that the smaller size of male gametes allows males to reproduce at a faster rate than females, so that whereas a female's reproductive success is constrained by the rate at which she can produce eggs, a male's reproductive success is limited solely by the number of matings he can achieve. The ratio of sexually receptive females to sexually active males (termed the "operational sex ratio": Emlen & Oring 1977) is thus likely to be less than one in many species. Sexual selection theory has subsequently been expanded and refined, particularly with respect to parental expenditure and reproductive rates (*e.g.* Trivers 1972; Knapton 1984; Clutton-Brock & Vincent 1991).

Although Darwin showed remarkable insight in explaining how differential investment in gametes could relate to differences in the general reproductive behaviour of the two sexes, particularly to aspects of mate choice, he did not seem to realise the importance of parental

care in shaping sexual selection. Williams (1966a,b) recognised that although differential investment in gametes can predict differences in reproductive rate for species with no parental care, the existence of any level of care beyond the mere production of eggs and sperm can alter this balance. Trivers (1972) expanded this concept further, stating succinctly that "what governs the operation of sexual selection is the relative parental investment of the sexes in the offspring". He thus re-defined Bateman's argument, recognising that parental care can potentially affect not only the adult sex ratio but also the mating system, which can vary from polygyny to polyandry.

Harsh or unpredictable environmental conditions, or high levels of predation or resource competition, usually lead to a situation where the benefits of parental care are large; in these cases one or both parents will be selected to provide parental care in the form of feeding or protection, and this will affect the operational sex ratio (Clutton-Brock 1991). In species where the male is responsible for all parental care, and the female's contribution is solely the production of eggs, one might expect that males would be the scarce resource; females would be more brightly coloured and compete for males, and males would be the choosier sex. However, the direction of mating competition differs between species. Clutton-Brock & Vincent (1991) suggested that the variation in mating systems occurs because in few species does parental care by the male depress his potential reproductive rate below that of the female, and concluded that "the potential rates of reproduction by males and females thus provide a basis for predicting the direction of mating competition in the two sexes and thus the direction of sexual selection".

Clutton-Brock & Parker (1992) recognised that the relative reproductive rate, although determined primarily by the operational sex ratio, can be affected by factors other than the fitness costs of rearing offspring. Such factors include the distribution of the two sexes in time and space (Sutherland 1985; Clutton-Brock & Vincent 1991); biases in the sex ratio at birth or hatching (Clutton-Brock & Parker 1992); the relative benefits to males and females of acquiring a superior mate (Burley 1977, 1986; Andersson 1982a,b); adaptations to competition, such as mate guarding (*e.g.* Parker 1974; Elwood & Dick 1990; Petrie 1992a; Dick & Elwood 1993); and sex differences in development time or life expectancy

(Breitwisch 1989; Clutton-Brock & Vincent 1991), which may reflect the relative costs of competition (Clutton-Brock 1991).

The tendency for an individual to display parental care can depend not only on the requirements of the offspring, but also on the probability that that individual is the genetic parent of the offspring. In particular, it has long been recognised that a close association exists between the mode of fertilisation (internal or external) of a female's eggs and the degree of paternal care shown towards the resulting offspring. For example, uniparental male care (generally in the form of egg-guarding) predominates among fish (Blumer 1979), the majority of which have external fertilisation. Trivers (1972), Blumer (1979) and Perrone & Zaret (1979) suggest that since a male's confidence of paternity is higher with external fertilisation, there is a higher probability that he will be increasing his inclusive fitness by providing parental care. This explanation however has been demonstrated to be inadequate in certain situations (*e.g.* Grafen 1980; Baylis 1981), such as in species where "sneaky breeders" are successful in fertilising eggs (*e.g.* the bullfrog *Rana catesbiana*, Howard 1978, Arak 1984; and the blue-headed wrasse *Labrus sp.*, Warner RR 1984).

At least two alternative theories have been expounded to account for the relationship between external fertilisation and paternal care. Firstly, since a female deposits her gametes before the male, she has the opportunity to desert, leaving the male with a choice of either deserting as well (thereby losing all of his inclusive fitness in that clutch) or caring for the clutch alone (Trivers 1972; Dawkins & Carlisle 1976). An alternative and perhaps more convincing explanation, however, is that decisions about which sex will provide care are based on sex differences in the costs of caring (Williams 1975; Gross & Sargent 1985; Clutton-Brock 1991). In many species (*e.g.* the stickleback *Gasterosteus aculeatus*) a single male can successfully fertilise and guard the eggs of several females, but the reverse would not be possible since the energetic costs of spawning are generally much higher for females than for males (Wootton 1984).

In contrast, fertilisation in birds and mammals takes place internally. In these species, where a female has the ability to store sperm from copulations with a number of different males, there is a lower probability that any particular male is the genetic father of any offspring

produced by that female. Selection would act against him providing care for offspring which may not be his own, and the female may consequently be solely or predominantly responsible for the brood. Direct male parental care has been reported in fewer than 5% of mammal species (Clutton-Brock 1991), and its rarity in this group is due to the existence not only of internal fertilisation but also of viviparity. The male cannot provide care for the offspring during the period of gestation (although he might be able to feed the female); similarly lactation is entirely the responsibility of the female. In general therefore the male has no parental duties during the offspring's early development, which provides greater opportunity to acquire additional mates, and it is not difficult to imagine how a polygynous mating system can arise from this situation.

Male care is relatively common however among a few mammalian groups, including the primates and the carnivores (Kleiman 1985; Clutton-Brock 1989). These species tend to be social rather than solitary, with monogamous or communal breeding systems (Kleiman & Malcolm 1981); the infants are generally born in a fairly altricial state, and require additional parental care for survival to reproductive age. Since in endotherms the number of offspring parents can produce is constrained by their ability (i) to keep the young warm, and (ii) to find sufficient food (or produce sufficient milk) for the young (Lack 1954, 1968), males may achieve higher overall reproductive success by providing care than by searching for extra mates.

The operation of these constraints is particularly widespread among birds, where biparental care is the norm. Over 90% of bird species are monogamous (Lack 1968), and all exhibit some form of parental care of the chicks apart from the megapodes and the brood parasites (Kendeigh 1952). A male megapode builds a large mound of rotting vegetation, into which the female lays her egg, which is then covered over by the male (Jones 1991). He monitors the temperature of the "nest" and adjusts it by scraping away or adding material, but once the precocial chick has hatched it climbs out of the mound and thereafter receives no parental attention. Nest and brood parasites deposit eggs or chicks into another individual's clutch or brood, thus avoiding the costs of parental care (see Section 3.4 and Chapter Six).

Parental care is necessary in most species as chicks hatch at a relatively early stage of development and require a high level of investment in the immature state; male birds also have far greater opportunity to invest in young (*e.g.* by incubation and collecting food for nestlings) than male mammals. The length of time spent in each stage of development (*i.e.* as eggs/dependent juveniles/sub-adults/adults) is linked to the life history trade-offs and mortality patterns of the species (Harvey & Clutton-Brock 1985; Welty & Baptista 1988; Harvey *et al.* 1989; Clutton-Brock 1991); animals with a longer life expectancy might be expected to spend longer in the immature stages. Similarly in species where large adult body size is important for increased survival or mating success, a longer juvenile period allows more growth before maturity is reached.

Many authors have considered the trade-off between time spent in the egg and time spent as a juvenile (*e.g.* Sibly & Calow 1986; Baker 1990, 1992). Shine (1978) proposed the "safe harbor" model, which in essence suggests that under natural selection, the duration of the safest developmental stages will be maximised, and those with the highest rate of instantaneous mortality will be minimised. This model however has been shown to have several rather simplistic assumptions (Clutton-Brock 1991). In particular Shine assumes that egg size does not affect juvenile survival, which is clearly unrealistic, and the hypothesis has been amended subsequently by Sargent *et al.* (1987) to allow for a negative correlation between egg size and juvenile mortality.

If chicks from smaller eggs hatch at a relatively early stage of development, with correspondingly lower chances of survival, they will require a higher level of parental care before they reach independence. As described above, the vast majority of monogamous birds with altricial young display biparental care (Skutch 1976; Lack 1954, 1968; Silver 1985), although males and females need not necessarily contribute equally. In contrast, with very few exceptions (*e.g.* some hummingbirds) uniparental care is shown by species with comparatively large, well-yolked eggs which hatch into precocial chicks. The young are therefore generally capable of walking and feeding themselves from the start, and a single parent can care for the brood without assistance from a partner.

Uniparental male care in birds is extremely rare (Ridley 1978), and is associated with several different mating systems including polyandry (one female mates with more than one male: *e.g.* the jacañas, Erkmann 1983), harem polygyny (one male defends several females: *e.g.* the ostrich, *Struthio camelus*, Bertram 1978) and monogamy (one male partners one female: *e.g.* the kiwis, Clutton-Brock 1991). Species displaying uniparental female care are more common (Kendeigh 1952; Welty & Baptista 1988; Clutton-Brock 1991). The vast majority are polygynous with precocial young; exceptions include some ducks (Kear 1970) and grouse (Wiley 1974) and a few species of hummingbirds (Kendeigh 1952).

The family Phasianidae however provides typical examples of polygynous, nidifugous birds with uniparental female care (Johnsgard 1986). They are cursorial, ground-nesting birds; in spite of their large egg size, they have relatively short incubation periods - an adaptive response to the particularly high risk of clutch predation suffered by pheasants (Lack 1968; Welty & Baptista 1988).

In some species (*e.g.* the Florida scrub jay *Aphelocoma coerulescens*: Woolfenden 1975) chicks are not raised solely by their parents, but assistance may be provided by adults of one or both sexes. This type of parental care is termed cooperative or communal breeding (Ricklefs 1975; Emlen 1984; Brown 1987); individuals may mate monogamously, polygamously or promiscuously. The specific nature of helping behaviour depends on the ecology and social system of the species concerned. Communal breeding is often shown by colonial birds with a high degree of philopatry, so that helpers are related individuals (Krebs & Davies 1987). The concept of "helpers at the nest" and other forms of alloparental care will be discussed further in Chapter Six.

1.3.2 Definitions

It is useful at this point to provide some formal definitions of the terminology used in this discussion of parental behaviour, since the expressions used by previous authors are not always synonymous and are thus liable to be confusing. Trivers (1972) originally defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the

parent's ability to invest in other offspring". This definition is often taken to imply a decrease in investment in *future* young (*e.g.* Clutton-Brock 1991), but of course must also include the current offspring's broodmates, and any young of previous breeding attempts in which the offspring's parent is still investing.

"Reproductive value" is defined as the number of offspring that an average organism in a particular age class can expect to have over the rest of its life under the conditions prevailing, discounted back to the present by the current population growth rate (Fisher 1930; Stearns 1992). The reproductive value of an individual can thus be estimated from the value of its age class. The expected number of *future* offspring produced, after the current breeding attempt, is termed the "residual reproductive value" (Williams 1966b; Stearns 1992); investment in the current breeding attempt is therefore likely to be inversely related to the residual reproductive value.

As an individual grows older its residual reproductive value will decline, since the expected number of remaining breeding opportunities decreases. Both parental investment and residual reproductive value are composed of many different factors (for example, time and energy expended in food gathering, risks taken in brood defence, and loss of extra mating opportunities), and comparison of these various components would involve dealing in different units of measurement, or "currencies" (Knapton 1984). Although Trivers (1972) does describe a common currency for all investments - "I measure the size of a parental investment by reference to its negative effect on the parent's ability to invest in other offspring" - it is not generally possible to obtain an empirical value for the residual reproductive value of an individual, and hence "parental investment" cannot be realistically quantified in practice (Knapton 1984; Clutton-Brock 1991).

"Parental investment" is generally used now in a less restrictive manner than Trivers' definition (*e.g.* Krebs & Davies 1987); Clutton-Brock (1991) defines it as "any characteristics or actions of parents that increase the fitness of their offspring at a cost to any component of the parent's fitness". This definition encompasses a wide range of possible costs to the parent, such as survival, growth, fecundity and subsequent mating success (Gross and Sargent 1985), as well as costs to (or lack of increase in) the fitness of other

offspring (Clutton-Brock 1991). The inclusion of somatic as well as purely reproductive costs provides the researcher with a wider range of variables from which to record measurements, and although the previous difficulties of comparing various fitness components are not overcome, any measurement of variation in parental fitness costs can give a valuable indication of relative parental investment. Throughout this thesis the use of the term "parental investment" implies the definition given above.

An important point to note is that there is no necessary correlation between the size of parental investment in an offspring and its benefit for the young (Trivers 1972; Evans 1990; Clutton-Brock 1991). For example, consider a parent bird collecting food for its nestlings. If food becomes scarce, the parent may fly further to search for food (*i.e.* it increases its parental effort), but it may not be able to bring back as much food to the nest (*i.e.* the benefit to the young will decrease). Environmental factors can thus play a major role in the relationship between the cost of an action to the parent, and its benefit to the offspring.

Clutton-Brock (1991) has also clarified the differences between several other parameters of parental behaviour, and I aim to adhere to his definitions. "Parental investment" usually refers to investment in individual offspring, while the total costs for all offspring are termed "parental effort". Some authors have used "parental investment" to denote both parental investment (as defined here) and parental effort, and "parental effort" is also occasionally used to mean "parental expenditure" (see below). Parental effort is combined with "mating effort" to form the "reproductive effort" of an individual (Low 1978; Alexander & Borgia 1979; Krebs & Davies 1987).

The behavioural expression of parental investment (or parental effort) is in the form of "parental care". This term implies nothing about the costs to the parent, but describes any behaviour that appears likely to enhance the fitness of a parent's offspring. Parental care can include not only the care of eggs and chicks, but also parental behaviours before the offspring leaves the parent's body, such as the preparation of the nest, and the production of large, well-nourished eggs. It is important to stress that only *parental* behaviours are involved, although it can be difficult to disentangle parental effort from mating effort in some species. For example where nuptial gifts are provided by a male, they may enhance the

female's (and hence offspring's) condition, as well as ensuring him a mating opportunity (see *e.g.* Thornhill 1976; Nisbet 1973, 1977; Thornhill & Alcock 1983).

"Parental expenditure" is defined as the expenditure of parental resources on parental care of one or more offspring (Clutton-Brock 1991). This includes both the expenditure of energy (*e.g.* in egg production or lactation) and time (*e.g.* in egg guarding or collecting food for nestlings).

Although parental care can be expressed by a wide variety of behaviour patterns, it is possible nevertheless to differentiate types of care according to their relationship with brood size. Lazarus and Inglis (1978, 1986) have distinguished two modes of parental investment which they term "shared" and "unshared", referring to how the benefit of a particular parental act is distributed among the offspring in a brood. These categories are explained in more detail below.

1.3.3 When (and how much) should parents invest?

Trade-offs

Parental investment can be manifested in many ways, showing variation in the amount, timing and form of parental care expressed. Whether or not an individual undertakes a parental act will depend upon the costs and benefits of alternative strategies, with respect to the particular ecological and life history constraints on the individual. An animal will be selected to show some level of parental care whenever the inclusive fitness benefits gained by doing so (*i.e.* by increasing the offspring's chance of survival and reproduction) exceed the costs incurred by losing additional opportunities to mate (Hamilton 1964; Trivers 1972). Williams (1966a,b) described how the mating system will be determined by the relative costs and benefits of each mating strategy to males and females - for example, selection will act upon a male to provide paternal care only if he gains a higher reproductive success by doing so than if he deserts his partner and attempts to increase his rate of copulations (see *e.g.* Maynard Smith 1984).

Similarly, costs and benefits apply to investment in clutch or litter size, and egg or neonate size. The traditional starting point for consideration of clutch size evolution in birds is known as the "Lack clutch", which is simply the clutch size that gives rise to the most fledglings, assuming that nestling mortality increases with increasing clutch size (Lack 1947, 1954). However, observed clutch sizes are rarely the same as those predicted from theoretical calculations, and many subsequent models have been developed to explain deviations from the Lack clutch (*e.g.* Klomp 1970; Lindén & Møller 1989; Stearns 1992).

Factors which may reduce clutch size to below the predicted optimum include: (i) trade-offs with parental fitness (*e.g.* parental mortality, or the ability of the parent to invest in subsequent reproductive attempts: Williams 1966a,b; Pianka 1976; Sibly & Calow 1986); (ii) trade-offs with offspring fitness (*e.g.* offspring survival or future reproductive success: Williams 1966b; Smith & Fretwell 1974: Andersson 1978); (iii) changes in environmental influences (*e.g.* increasing predation levels, or declining vegetative cover: Stearns 1992); (iv) parent-offspring conflict (*e.g.* conflict between parents and offspring of previous breeding attempts over the size of investment in the current clutch: Trivers 1974; Stearns 1992); and (v) nest parasitism (*i.e.* parents are laying fewer than the optimum number of eggs, as an insurance against the possibility that the clutch will be parasitised: Power *et al.* 1989).

Although observed clutch sizes are generally smaller than the predicted optimum (Klomp 1970), other factors can influence clutch or litter size in different ways. For example, both brood reduction and selective abortion can result in enlarged clutch or litter sizes, since the number of offspring can be reduced after hatching or birth to the optimum number depending upon environmental conditions (*e.g.* Wilson 1975). In addition, clutch size and/ or propagule size may be restricted by physiological or ecological constraints: for example, selection may favour a particular clutch size so strongly that parental resources are channelled into increasing egg size, or *vice versa* (Clutton-Brock 1991).

The trade-off between offspring size and number has received much attention, particularly since the model produced by Smith & Fretwell (1974). They predicted that the relationship

between parental effort and offspring fitness will be convex in shape, and that the optimum level of expenditure occurs at the point where a straight line from the origin touches the curve at a tangent (see Figure 3.1). Although this model provides a useful basis for analysis of clutch *vs.* propagule size trade-offs, in practice the relationship is likely to be considerably more complex (see Clutton-Brock 1991; Stearns 1992). For example, the "optimum" point refers only to the optimum for the parent, and therefore does not take into account some of the factors discussed above, such as the effects of variation in propagule size on offspring fitness. In addition, the relationship between parental effort and offspring fitness need not necessarily be a simple convex curve; for example, there may be different optimal levels of expenditure for different-sized individuals in a population (*e.g.* Sargent *et al.* 1987).

A range of factors other than clutch size can potentially affect propagule size (Clutton-Brock 1991). Larger eggs generally hatch chicks of a higher quality (for example, the eggs of precocial species are relatively larger than those of altricial species), and higher quality offspring may be better able to withstand a poor quality environment or patchy resource availability. Life history constraints, such as hibernation, and inter- and intra-specific competition, may also select for larger eggs or neonates; yet propagule size may be constrained by parental body size or genetic quality. The duration of each developmental stage may be determined by relative selective pressures such as predation (*cf.* Shine's (1978) "safe harbor" hypothesis, outlined in Section 1.2.1), and this will in turn control the stage at which an egg becomes a chick, or an embryo becomes a neonate. Propagule size must also be affected by total parental expenditure and the duration of parental care, which are in turn influenced by the residual reproductive value of the parent (see below). The factors outlined here should not be considered in isolation, as many of them are obviously likely to be inter-correlated. Egg and clutch size in particular relation to peafowl will be discussed further in Chapter Three.

Investment in relation to reproductive value

For an individual of a multiparous species, parental expenditure has to be allocated not only within each particular breeding attempt, but effort also has to be divided among subsequent

attempts over its lifespan. It might be expected to vary parental expenditure according not only to resource availability, but to its own residual reproductive value as well as to the reproductive value of the current offspring (Williams 1966b; Pianka 1976; Curio 1983; Winkler 1987). Williams predicted a negative correlation between reproductive effort and residual reproductive value: in other words, older individuals should invest a greater proportion of the resources available to them than younger ones, since reproduction may be more costly to young breeders. For example, Pugesek (1981) found that older California gulls *Larus californicus* have higher reproductive success, apparently because they expend greater parental effort than young individuals.

The difference in expenditure by old and young parents has at least three explanations (Clutton-Brock 1991). Firstly, energetic costs may be greater (leading to reduced survival) in novice or young breeders, even when they have smaller clutch or litter sizes (Clutton-Brock 1984). Secondly, if individuals continue to grow after reaching reproductive age, a breeding attempt may delay or prevent attainment of maximum size, thus reducing reproductive success over the lifespan (Gross & Sargent 1985; Berglund & Rosenqvist 1986). Finally, if survival declines with age, a given risk of dying as a result of breeding is a larger cost to young animals than older ones, especially in multiparous species (Pianka 1976; Curio 1988).

It is difficult however to distinguish adaptive strategies of parental expenditure from the ecological consequences of variations in food availability or parental ability. Younger parents may in fact be investing a greater proportion of their resources in a breeding attempt than older ones, in spite of their lower reproductive success (Fagen 1972) - for example, breeding or foraging skills may increase with experience (Lack 1966). For example, Begon & Parker (1986) envisaged a situation in which, if the resources available for reproduction are fixed at the outset and there is a significant mortality risk to the parent between clutches, selection would favour larger egg and clutch sizes early in the lifespan. Thornhill (1989) was able to demonstrate that offspring defence by red junglefowl hens increases with hen age but not with parental experience, but very few other studies have successfully managed to separate these effects.

Williams (1966b) predicted that an individual should also increase parental effort with increased reproductive value of its offspring. This value will depend upon several factors including parent-offspring relatedness (Winkler 1987; Montgomerie & Weatherhead 1988), brood size (Lack 1954; Smith & Fretwell 1974; Lazarus & Inglis 1986), and offspring age and quality (Williams 1966a,b; Clutton-Brock 1991). Evidence that animals invest according to the degree of relatedness is provided by cooperatively breeding birds, in which "helpers at the nest" are older siblings of the nestlings (Emlen 1984; Woolfenden & Fitzpatrick 1984); and by ground squirrels, where the probability of giving an alarm call is proportional to the relatedness of the caller to nearby individuals in danger (Dunford 1977; Sherman 1977). In contrast, care of unrelated individuals is rare (see Chapter Six).

Parental expenditure might be expected to be positively correlated with brood size, since larger broods increase the parent's genetic contribution to subsequent generations. However, parental expenditure is adjusted not only to its benefit for the parent, but also to its benefits for the offspring, and its level will therefore depend upon the nature of the care (see shared and unshared parental investment, below). The effects of parental care on offspring fitness are also likely to confound predictions about investment in relation to the reproductive value of individual offspring. Older juveniles are worth more to the parent because they generally have a greater chance of survival to reproductive age than younger ones (Williams 1966b; Andersson *et al.* 1980); but as offspring grow older they become increasingly independent and capable of looking after themselves, thereby reducing the benefits of any particular level of parental care (*e.g.* Emlen 1970; Sargent & Gross 1985; Westmoreland 1989). Thus although reproductive value (and therefore parental investment) is expected to increase with offspring age, changes in the effect of care on offspring fitness are likely to favour a reduction in parental expenditure.

The observation that individuals are likely to invest more in offspring of higher reproductive value was originally explained by Trivers (1972), who stated that a large initial investment "commits" the parent to a high level of continued investment. This argument has subsequently been proved incorrect, and is now known as the "Concorde fallacy" (Dawkins & Carlisle 1976; Boucher 1977), after the British investment policy in the Concorde

supersonic aircraft. Politicians justified further expenditure on its development, in order to minimise wastage of previous outlay, even though this strategy was not economically viable (Dawkins 1976). Similarly in animals, current parental expenditure should be adjusted to expected *future* gains, not to costs in the *past*; but previous investment may nevertheless be a useful indication of the remaining expenditure necessary to raise offspring to independence (Maynard Smith 1977; Curio 1987).

As with residual reproductive value, the problems of attempting to measure reproductive value are obviously immense; in addition, the reproductive value of any individual will be continually changing as the animal grows, matures and breeds. In biparental species, the care given by one parent will almost certainly depend upon the effort expended by its partner, and other factors (*e.g.* parental residual reproductive value, environment *etc.*) also have to be disentangled. Despite the enormity of these practical difficulties, Chapters Three, Four and Five attempt to predict how variations in offspring reproductive value might affect the level of parental expenditure.

Parent-offspring conflict

In all sexually reproducing animals, where individuals are not genetically identical, there are likely to be conflicts of interest; these might arise between parents, between parents and offspring, and between siblings within a brood. Trivers (1974) argued that, since the coefficient of relatedness (r) between parents and offspring is 0.5, an act of parental investment will cost the parent twice as much as the offspring. Consequently he predicted that the optimum level of parental investment for the parent is when the difference between parental cost and benefit is maximised, whereas the offspring optimum occurs when the difference between offspring cost (*i.e.* half the cost to the parent) and benefit is greatest. The offspring optimum will therefore occur at a higher cumulative level of parental investment than the parental optimum, leading to conflict between the two parties over when parental care should decline.

Trivers (1974) did not differentiate between parental and offspring benefit. Lazarus & Inglis (1986) modified Trivers' argument, showing how parent and offspring are in conflict over

the benefit of a given act of parental investment and not over its cost, since the cost to each (in terms of a decrease in the parent's future offspring, to which both are related by $r = 0.5$) is identical. They nevertheless arrive at the same general conclusion: parents will begin to reject offspring *before* the latter will accept rejection.

Shared and unshared parental investment

The manner in which investment in parental care varies with brood size will depend upon the effects of that care on offspring fitness. Lazarus & Inglis (1978, 1986) described two contrasting categories of parental care, "shared" and "unshared"*, differentiated by how the benefit of a parental act is allocated among the brood. "Shared" investment is divided between the offspring so that each receives only a portion of it (*e.g.* food brought by parents to nidicolous young), whereas the total benefit of an "unshared" parental act is simultaneously gained by each of the young (*e.g.* scanning for predators). It should be noted that these two modes represent the extremes of a continuum, and that there are many examples of behaviour patterns (*e.g.* incubation) which would be unshared in certain circumstances (*i.e.* with small clutch sizes, when each egg receives continual warmth) and shared in others (*i.e.* with large clutches, when the warmth received by an egg may depend upon its position in the nest) (*sensu* Lazarus & Inglis 1986).

Where there is a certain minimum level of expenditure necessary for offspring survival, shared components of parental investment are predicted to be positively correlated with brood size (Lazarus & Inglis 1986; Montgomerie & Weatherhead 1988). In contrast, the relationship between brood size and unshared investment will depend upon the nature of the parental act. Probably the majority of cases of unshared parental investment involve protection of the young from predators, and expenditure takes the form of vigilance, warning calls or active defence (Lazarus & Inglis 1978).

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* Altmann *et al.* (1977) refer to the first category as "depreciable" and the second as "non-depreciable" parental care; whereas Wittenberger (1979a) uses the terms "non-shareable" and "shareable" respectively. Throughout this thesis the terms and definitions given by Lazarus & Inglis (1978, 1986) will be used.

If a predator typically takes a single chick when it strikes ("fixed loss"), such as is common with nidifugous species, then the benefit to the parent remains the same whatever the brood size, and expenditure is predicted to be independent of the number of offspring (Lazarus & Inglis 1986). If loss of the whole brood is the norm ("brood loss"), expenditure should increase with brood size, since the benefit to the parent is greater for larger broods (Barash 1982; Lazarus & Inglis 1986). These predictions can be complicated, however, by the effect of what Lazarus & Inglis (1986) have termed "present cost"; if a parent is killed or injured while defending its brood, the current offspring would be very likely to perish without parental care. Thus the cost to the parent of such high-risk activities increases with brood size; depending upon whether the benefit increases simultaneously ("brood loss") or is independent of brood size ("fixed loss"), the resulting relationship between brood size and the level of expenditure may be weakened (Lazarus & Inglis 1986).

The hypotheses of shared and unshared investment have been widely tested in the field (*e.g.* Caro 1987; Lessells 1987; Schindler & Lamprecht 1987; Sedinger & Raveling 1990; Coleman & Fischer 1991). However, brood size manipulations are often desirable in order to discover the real relationship between brood size and parental expenditure, otherwise there may be confounding effects of parental quality - *i.e.* superior individuals hatching larger broods and also expending greater parental care on them (*e.g.* Carlisle 1985; Windt & Curio 1986; Thornhill 1989).

Sons and daughters

Fisher (1930) concluded that although the numbers of each sex produced may not be identical, total parental investment in sons and daughters is always equal. This was not refuted until 1963, when Wilson & Pianka first suggested that it can be adaptive for parents to invest more heavily in one sex, if by doing so they receive a greater increase in parental fitness. The investment in each sex will depend upon both the relative effects of expenditure on sons' and daughters' fitness, and the level of resources that the parent is able to commit to parental investment at any particular stage.

In many mammals and a few birds, where body size and early growth affect the fitness of males more than females, it may well be adaptive for a parent to invest more heavily in sons than daughters (Trivers & Willard 1973; Clutton-Brock 1988; Stamps 1990; Clutton-Brock 1991). In polygynous species for example, a higher level of expenditure on a male offspring could enable it to achieve a larger adult size, be more successful in competition for resources or access to mates, and thus have increased reproductive success. From their long-term study of red deer *Cervus elaphus* on the Isle of Rhum, Clutton-Brock and his co-workers were able to test Trivers' and Willard's (1973) hypothesis and showed that dominant females in better condition are indeed significantly more likely to produce sons (*e.g.* Clutton-Brock, Guinness & Albon 1982; Clutton-Brock, Albon & Guinness 1984). Conversely, when parents are in poor condition or environmental pressures are severe, it would be more adaptive for an individual to invest in the sex that is cheaper to produce (usually daughters) or that has a less risky reproductive potential (again, usually daughters) (Trivers & Willard 1973; Gosling 1986a,b).

1.4 Conclusions

Reproductive value theory predicts that an individual should increase levels of parental investment as their own residual reproductive value declines, and as the reproductive value of its offspring increases (Fisher 1930; Williams 1966b; Trivers 1972). Hence expenditure is predicted to increase with both parental and offspring age. This simple model can be extended to account for various ecological, physiological and life history constraints, such as parental condition and experience, time in season, resource availability and predation pressure. Within individuals, there must also be trade-offs between the size and number of offspring, and for any particular clutch or brood size, additional models can predict how expenditure might be allocated among the offspring (*e.g.* Lazarus & Inglis 1986).

In the study presented here, the predictions outlined above are tested for feral peahens. Both material and behavioural measures of parental expenditure are used, and investment is studied from egg-laying until the chicks fledge. In addition to testing precise hypotheses, the general breeding behaviour of peahens at Whipsnade is investigated. Particular attention

is paid to pre- and post-hatch alloparental care, and several adaptive and non-adaptive explanations for the phenomenon are discussed.

CHAPTER TWO

GENERAL METHODS AND PRELIMINARY OBSERVATIONS

2.1 Study site and population

Whipsnade Wild Animal Park near Dunstable, Bedfordshire (Figure 2.1) holds a feral population of Indian peafowl, which I studied between October 1988 and October 1991. Individual birds have been brought into the Park from its opening in 1931, and have since bred successfully for many generations. Following a method described by Gaston (1975), I obtained population estimates by counting birds as they roosted at night. On clear moonlit nights in winter, individuals could be seen as silhouettes against the sky, unobscured by foliage (Plate 2.1). In this manner I estimated the population to be approximately 200 peafowl during the winter months of both 1988-89 and 1989-90 (no counts were made during the 1990-91 winter).

Plate 2.1. Silhouettes of peafowl in roost tree in January: adult males could be identified by their growing trains, but females and juvenile males were more difficult to distinguish.

Figure 2.1. Plan of Whipsnade Park Zoo, Bedfordshire. Drawing made on behalf of The Zoological Society of London, August 1987.

The peafowl population at the Park consists predominantly of the common Blue morph of *Pavo cristatus*, but there are also a few Black-winged (*P. c.* mut. *nigripennis*) individuals of both sexes, and hybrids of these two varieties. Until 1990 there were also two White females, but both of these died during the severe snows of January 1991.

The study site at Whipsnade covers 580 acres of chalky downland at the eastern end of the Chiltern Hills, consisting of a mixture of pastureland, rough scrubland and wooded areas, with several small lakes and ponds (Figure 2.1, Plate 2.2). Most of the Park's animals are kept as mixed-species herds in large fields, with supplementary feeding and access to shelters or heated sheds.

The Park is open to the public all year round between 1000-1830 in summer and 1000-1600 in winter, and visitors travel around the network of paths and roads on foot and by car. Approximately half a million people visit the Park each year, and at the height of summer there may be two thousand visitors per day. Consequently there are few areas of the Park that are totally secluded, although the steep slopes of the downs receive little disturbance.

Although the climate and environment of Whipsnade Wild Animal Park are obviously very different from India, the behavioural ecology of the feral peafowl population studied here does not appear to vary substantially from that reported for wild birds (see Section 2.2.1). The Whipsnade population is also much more accessible and open to observation, and can therefore provide a valuable means of investigating the parental behaviour of *Pavo cristatus*, provided that the data are interpreted with caution.

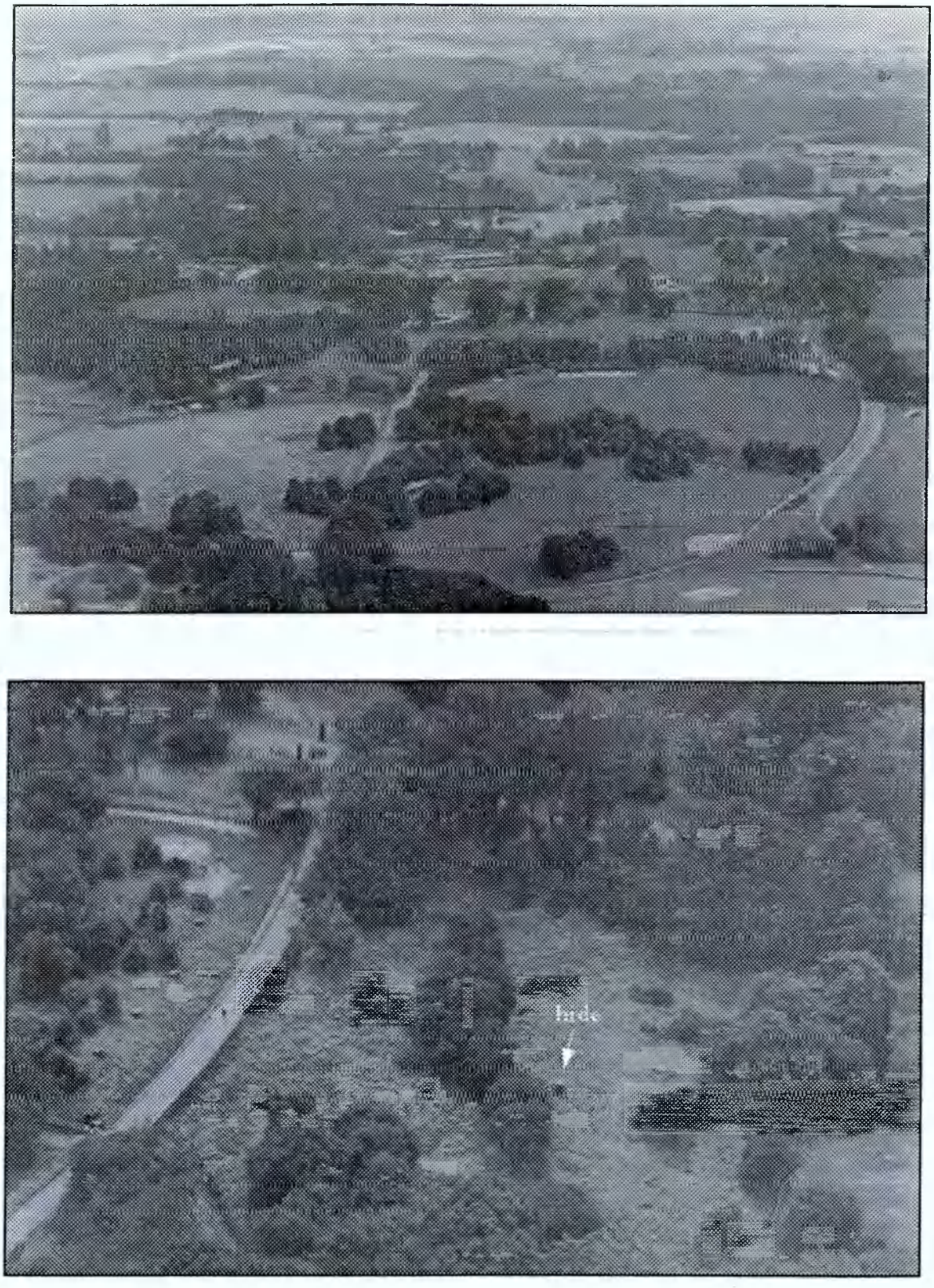

Plate 2.2. Aerial photographs of Whipsnade Wild Animal Park, Dunstable, Bedfordshire. 2.2*a*: Overview of the central region of the Park, showing the large fields and wooded areas; the trees at the bottom of the photograph mark the top of the steep downland slopes. 2.2*b*: Flint Pit Paddock, where many of the observations were made; the position of the hide is also shown. Photographs were taken with the kind assistance of the London Gliding Club, Dunstable.

2.2 Adults at Whipsnade

2.2.1 Daily behaviour of adult peafowl

The peafowl population at Whipsnade is allowed to roam freely over the entire Park, but for most of the year both males and females have a fairly limited home range, remaining faithful to just a few feeding sites and roosting trees. Although the birds are not actively fed, a considerable proportion of their diet consists of food put out for other animals. Consequently home ranges often centre around these "artificial" feeding areas, with closely associated roosting trees - usually oak, or similarly large trees with suitable roosting branches.

In an attempt to measure seasonal variation in male and female home ranges, I made regular surveys of the Park and recorded the location of each individual seen as a grid reference on a map. Individuals were identified by means of plastic leg rings (see Section 2.2.2). Surveys were completed at least once every fortnight between October 1988 and September 1989, and once every four or five weeks subsequently. Associations between individuals were also recorded: two birds were defined as "associating" if they were less than ten metres apart at the time of observation. By concentrating my observations around the middle of the day, when the birds are most likely to be sedentary (Navatheekannan 1984; pers. obs.), I aimed to maximise the number of individuals located in each survey. Although there were many occasions when particular birds could not be found, these surveys nevertheless provide a useful indication of seasonal and individual variation in home ranges.

During the winter months (approximately October to early January) the birds form large, mixed-sex roosts at night, but during the day the feeding groups tend to be predominantly single-sex. This situation changes from January-February onwards, as many of the adult males begin to clump together and defend territories in traditional lekking areas. Five major lek sites have been identified at Whipsnade, each consisting of between 4 and 10 display sites. These sites are defended from around February until August, hence during the day the territory-holding adult males are rather stationary, leaving their display sites only to feed,

drink and roost. Throughout the mating season territorial males often roost alone near their lek sites, while the rest of the population continues to spend the night at the traditional roost sites.

In contrast to territory-holding males, the mobility of females, juvenile males and "floating" males (*i.e.* adult males that do not hold a lek display site: Petrie *et al.* 1991) is considerably increased during the summer months. For example, a female's winter home range is often based around one or two lek sites, but during the early breeding season (April-May) she may visit several leks within a single day, and several males within a single lek (Petrie *et al.* 1991, 1992; pers. obs.). Hens become less gregarious during this time, and are almost solitary from the onset of laying (Section 2.3.1). However, single broody females are frequently accompanied by two year old and floating males. These males will preferentially approach nesting hens and those which had left the nest to forage, and on many occasions this attentive behaviour apparently amounted to "harassment". Some detailed observations of, and suggested explanations for, the harassment of nesting hens is given in Section 3.5.

The daily routine of peafowl at Whipsnade follows that of their wild counterparts (see Navatheekannan 1984), with the population descending from the roosts at dawn, or later if the weather is wet. As the birds in the Park take advantage of supplementary feeding, the main early morning and late afternoon foraging periods are fairly short (approximately 1-2 hours' duration), and the bulk of the day is usually spent preening, occasionally wandering in search of food, or just "loafing" in small groups. This pattern remains fairly consistent throughout the year for non-breeding birds, but is obviously very different for reproductive individuals during the summer months. As described above, lekking males are present on their territories for most of the day, displaying whenever a female is in the vicinity, and will often roost in trees adjacent to their lek sites. Incubating females generally spend nearly 24 hours a day on the nest, leaving it only to feed (Section 2.3.1). Hens commonly make two foraging trips per day, one in late morning and a second in mid-afternoon, both of between 10-45 minutes duration depending on the accessibility of food sources. As their broods hatch, the majority of the females' day is devoted to walking along and searching for food,

but as the chicks grow older their daily routine becomes more similar to that of non-breeding hens (see Section 2.4.1 and Chapter Five).

2.2.2 Identification of adults

Peafowl at Whipsnade were caught over the winter months (October - April) of 1987-1991, with the aim of maximising the number of individually identifiable birds in the population, as well as measuring morphological variation and extracting blood for DNA fingerprinting. This work was carried out both for the purposes of the study described here, and for the research into peafowl mating behaviour by Marion Petrie, Tim Halliday *et al.*.

Eight large cage traps from Agriframe were used; these were constructed from lightweight aluminium poles covered in strong plastic netting, with a side-hinged door at one end. The door could be closed from a distance by means of a long piece of string which was camouflaged wherever possible (*e.g.* by leaves), as the peafowl were extremely wary of novel objects. Cages were baited with cut maize and occasionally mixed peanuts and raisins; at any particular trap location, attempted capture followed 1-3 days of pre-baiting. Trapping was achieved by closing the door with the string, then entering the cage and putting the birds into large hessian sacks. The peafowl were then either processed immediately, or turned out into a large holding pen to await marking.

Two people were generally required for the processing of captured birds, one to take measurements and the other to restrain the bird. Individuals were identified by means of plastic leg rings; either by one or two spiral rings in a combination of colours (a range of nine colours was used: black, white, red, yellow, green, dark blue, light blue, mauve and orange), or by a numbered Darvik ring. Unless concealed by mud or vegetation, individuals could normally be identified with a telescope at up to 100 metres, and the coloured rings were distinguishable from even greater distances.

Each captured bird was weighed in its sack using a large balance, and a range of morphological measurements was taken as described in Table 2.1. "Tarsus length" refers to the distance from the joint between the fibula and the tarsometatarsus to the tip of the third digit on the right foot, and "wing length" to the distance from the carpal joint to the tip of the

longest primary feather on the right wing. Blood was then extracted from a superficial brachial vein for subsequent DNA analysis by Olivier Hanotte and Terry Burke at Leicester University. A 0.8mm bore needle was used to puncture the vein; the resulting droplet of blood was drawn out into three 4µm capillary tubes, which were then placed in buffer solution.

Bird number	14	Bill length (mm)	41.5
Ring colour/number	B27	Bill depth (mm)	15.1
Date captured	October 1988	Crest length (mm)	53.1
Date of hatch	≤ 1985	Spur length (mm)	7.2
Weight (kg)	3.320	Claw length (mm)	17.6
Tarsus length (mm)	198.0	Total ectoparasites on head per minute	0
Wing length (mm)	430.0		
Tail length (mm)	400.0	Ectoparasites drinking at eye per minute	0
Head length (mm)	80.9	Blood taken	3.0 c.t.
Notes	Leucistic female. Caught alone, in Flint Pit Paddock. Returned to FPP. First caught December 1986, ringed Red/White.		

Table 2.1. Example of morphological measurements taken on adult peahens at Whipsnade. Additional measurements were recorded for males (*e.g.* train length; number of upper tail coverts). Birds were measured in conjunction with M. Petrie and others.

Following marking and measuring, birds were released at their point of capture. Care was taken not to separate peahens from their young, and to minimise time spent in the holding pen. These precautions aimed to reduce the risk of either disrupting the relationships between captured individuals and their usual social groups, or socially integrating birds in the pen which would otherwise have been unfamiliar in the park. During the trapping seasons of 1989-91, males were held in separate pens from females and their offspring.

2.3 Nests at Whipsnade

2.3.1 Ecology and nesting behaviour

The first attempted copulations were seen at Whipsnade during March, and the first successful mating during mid-April (Petrie *et al.* 1991). Peahens began to lay eggs from

early May onwards, and at the beginning of the laying season there was a fairly high number of "dump-nests" and single abandoned eggs (this phenomenon will be discussed in detail in Chapter Three). The preferred nest cover appeared to be thick nettles, but nests were also found in long grass, under dense bushes, and occasionally in more exposed sites such as fairly short grass (Plate 2.2). Some hens even nested in the straw of other animals' shelters. The distribution of nests around the Park did not appear to bear any relation to the distribution of males' territories, and a number of hens laid some distance outside their normal winter home ranges.

The nesting period extended from May until August or September, at least partly because a high level of predation resulted in a large proportion of hens re-nesting. Known predators of peahen eggs are birds, especially corvids, and small mammals such as stoats and weasels. An egg attacked by a bird tended to have a large hole pecked in the side, so that the contents could be easily consumed, whereas a mammal would either completely destroy the shell or remove the egg and attempt to carry or roll it back to its burrow (pers. obs.). The majority (at least 75%) of predated eggs seen during my study period seemed to have been attacked by birds rather than mammals.

From the few data available it appears that females generally laid their eggs in the afternoon, at intervals of two days. Incubation began as the clutch was complete or nearly complete; incubated clutch sizes ranged from one to twelve, and hens with larger clutches (more than five eggs) were always seen to start incubating by the fifth or sixth egg. Clutches were incubated for 28-31 days, and the first broods hatched from early June (see Section 2.4).

Plates 2.3*a-f*. Typical nest sites at Whipsnade. 2.3*a,b*: The majority of nests are made in nettle clumps: *(a)* peahen nesting in thick nettles (early season); *(b)* hen sitting in sparse, dying nettles (late season).

Plate 2.3*c,d*: Nests in long grass: *(c)* female sitting; and *(d)* a clutch of four eggs.

Plate 2.3*e,f*: Nest sites at Whipsnade: *(e)* nest in dense thistles, showing female's entry and exit path; and *(f)* more open nest, laid amongst dead wood.

Peahens at Whipsnade seem to be fairly consistent in the size, shape and colour of eggs laid within a single clutch. However, in a considerable proportion of nests an egg (or eggs) appeared which was inconsistent with the rest of the clutch, or was laid out of synchrony with the usual two-day interval. Both these anomalies, and the occurrence of abnormally large clutches, provides evidence for the existence of intraspecific nest parasitism within the population. This strategy will be discussed further in Section 3.4.

2.3.2 Identification of nests and eggs

Throughout each nesting season (April - September), all likely areas in the Park (*i.e.* most of it!) were regularly searched for nests. Each area was covered at least once a week in 1989 and 1990, and once every two or three weeks in 1991, by walking through it, using a long bamboo cane to move aside the nettles and other vegetation. This method enabled approximately 85% of the nests to be discovered; others were found by following lone broody females back from their foraging trips. Broody hens were usually easily distinguishable from non-breeding hens by their general appearance and behaviour: females with nests were nearly always alone, and marched or ran to and from the feeding grounds. Their neck feathers were fluffed out while the rest of their plumage often appeared bedraggled, and they would frequently give the honking calls described in Section 1.1.2. Many nests and incubating hens however proved extremely difficult to locate, and at least a quarter of the nests were not discovered prior to hatching.

For each nest located, data were recorded as shown by the example in Table 2.2. Eggs were individually marked using indelible ink, weighed using a 300g Pesola spring balance, and measured (maximum length and width in mm) using Vernier calipers. An index of egg volume was calculated using the formula $V = [length \times (width)^2 \div 1000]$ cm^3, and throughout this thesis the term "egg volume" implies the value of this index. Photographs were taken of both individual eggs and whole clutches next to a scale (Plate 2.4), and the rough temperature (warm/cool/ cold) was felt by hand.

Nest	WW	Subsequent visits	Notes on visits
Date start incubation	~ 9.7.90.		
Date hatched/deserted	7.8.90.	16.7.90 (1615)	MO first seen sitting 16.7.90
Date recorded	17.7.90	17.7.90 (0930)	Eggs marked (see left)
Time	0930 (warm day)	19.7.90 (1115)	Hen absent. 5 eggs, all warm
Nest site description	Pigmy hippos shed	23.7.90 (0710)	Hen sitting
Nest site grid ref.	ZZXOd	26.7.90 (1645)	Hen sitting
Vegetative cover	24" nettles by shed wall	29.7.90 (1440)	Hen sitting/turning eggs (5 eggs)
Hen in attendance	Mauve Orange	1.8.90 (1030)	Hen sitting
Hen sitting or absent	Sitting	5.8.90 (1130)	Hen sitting
Clutch size	5	6.8.90 (1525)	Hen absent; eggs i,ii,iii,v pipping
General notes	Hen v. defensive, honks, displays.	8.8.90 (0805)	Eggs WWi, ii, iii, v have hatched; egg WWiv in nest whole (cold)

Egg	Weight (g)	Length (mm)	Width (mm)	Photo frame	Temp-erature	Notes on eggs
WWi	100	67.6	52.3	16,18	Warm	
WWii	108	70.0	53.6	16,18	Warm	
WWiii	98	68.3	52.1	16,18	Warm	
WWiv	97	70.1	51.0	17,18	Warm	Paler than rest of clutch.
WWv	96	65.7	52.3	17,18	Warm	Slightly darker, speckled.

Table 2.2. Example of data sheet for nests located at Whipsnade.

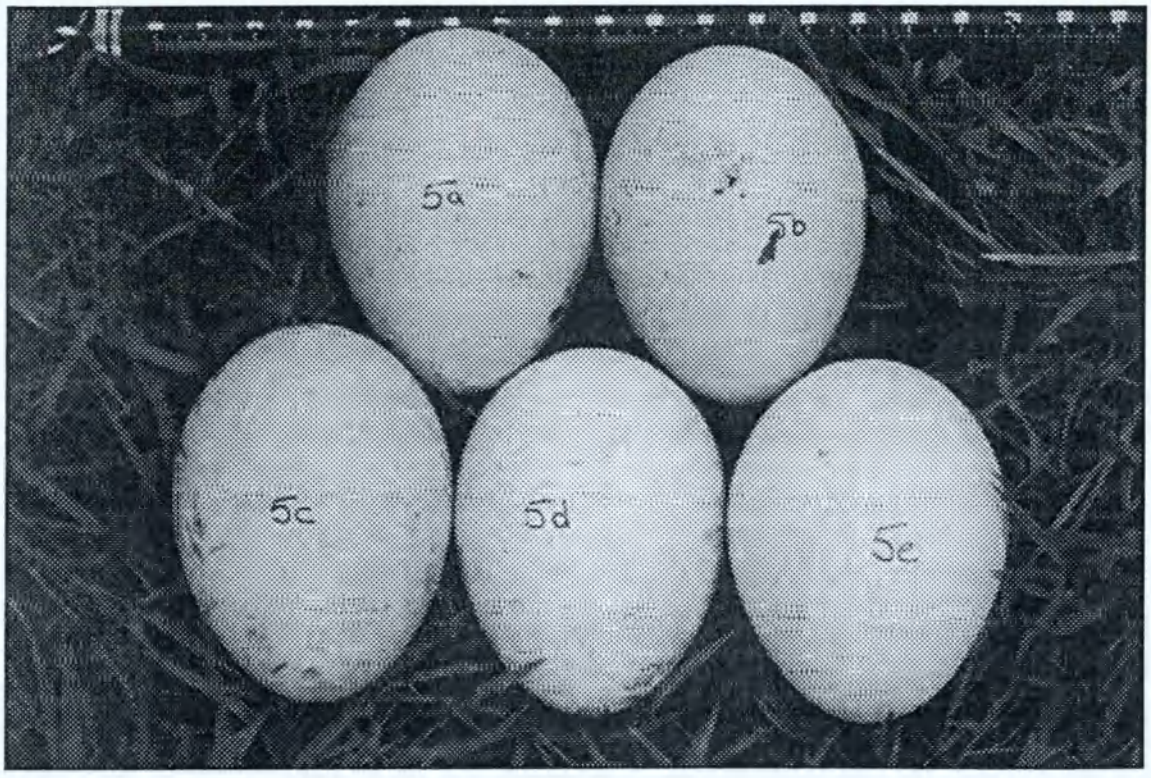

Plate 2.4. Photographic record of clutch and scale.
Original photographs were all life-size and taken in colour.

Nests were monitored from the time of discovery, and revisited if necessary when the hen was away to feed. Whenever possible the date of lay and of hatching was recorded for each egg, but in some cases these data were impossible to ascertain precisely. Both laying date and hatching date are measured in "May days" - *i.e.* the number of days after April 30th each year. The outcome of each nesting attempt was classified as "successful" (some or all eggs hatched) or "unsuccessful" (eggs were predated or the female deserted). All unhatched eggs were removed for dissection in the laboratory, and I estimated the approximate stage of embryonic development in those that were fertile. The thickness of both hatched and unhatched shells was measured using a micrometer, in order to discover whether shell thickness could provide any indication of the hen's investment in each egg. Unfortunately no useful data were obtained from these measures, since the variation in thickness between eggs was no greater than within-egg variation, and the technique was abandoned.

Parental investment in nesting will be discussed in greater depth in Chapter Three, which covers time budgets (see also Section 2.5.2), resource allocation, nest parasitism, dump-nesting, and interactions with other individuals. The behavioural ecology of nesting is also considered briefly in Chapter Six, in relation to pre- and post-hatch brood amalgamation.

2.4 Chicks at Whipsnade

2.4.1 Ecology and brooding behaviour

The development and behavioural ecology of peachicks in the wild has been described in Section 1.1.2, and apparently differs very little from that observed at Whipsnade. The first broods in the Park hatch from early June. Chicks hatch synchronously and females immediately (*i.e.* within 24 hours) lead their precocial broods away from the nest. Any eggs unhatched at that stage are abandoned, even if they are pipping. Such nidifugous behaviour is reported in many ground-nesting birds, with the suggested adaptive function of minimising the risk of predation (Welty & Baptista 1988).

For the first few days peahens keep their newly-hatched broods in isolation away from populated areas of the Park, but are then often seen to join with other parent females to form

"crèches" or "gang-broods". The occurrence of brood amalgamation and its associated behaviour patterns will be discussed further in Chapter Six, and its effects on parental behaviour are considered in Chapters Four and Five.

Chick development is very rapid, and within ten days or so of hatching young birds are capable of fluttering several metres over the ground. By the age of three weeks or so the primary flight feathers have started to develop, and peachicks are able to fly some distance in order to avoid danger. Up to that time females brood their young on the ground overnight, but once the peachicks are able to fly they can roost at night on low branches, protected under their mother's wings (Plate 2.5). As the chicks grow older they become increasingly independent, both while foraging during the day and in the nocturnal roosts. Peachicks remain with their mother for several months, but such close associations are usually terminated during their first winter, as adults and young join together in large foraging flocks. Some young females however are apparently still accompanying their mother at the start of the subsequent breeding season, although first-year males seem much more likely to have dispersed by that time.

Plate 2.5. Peahen brooding young chick under wing, on low branch of roost tree.

In common with their wild relatives, peachicks hatched at Whipsnade were vulnerable to a wide range of mortality factors (see below), and brood sizes were consequently reduced drastically from the time of hatching. The modal brood size at hatching was four, but rarely did more than one or two chicks from a brood survive until the subsequent breeding season, and it was extremely common for a female to lose the entire brood. If such a loss occurred early in the season, a hen might be able to re-nest and raise a second replacement brood, but a large proportion of breeding females at Whipsnade did not successfully raise any young over the season. Female breeding success will be discussed further in subsequent chapters.

Young chicks were particularly susceptible to predation, exposure, or accidental death. During my period of study, I found some chick bodies with the head bitten off, suggesting predation by a mustelid; some were discovered alone after a cold night, and had therefore probably succumbed to exposure; a few were found drowned in water troughs; and many other marked chicks simply disappeared. In 1991, white storks *Ciconia ciconia* were introduced into one particular paddock (Flint Pit Paddock), and I observed them several times attacking and killing young peachicks.

The degree of chick mortality declined at a few weeks of age as the young gained the ability to fly, but evidence from carcasses showed that even adult birds were vulnerable to larger predators such as foxes *Vulpes vulpes*. During the summer of 1989, the Park employed a gamekeeper who provided some control over the numbers of foxes and corvids. This predator regulation was not in operation during 1990 or 1991, and in 1991 two or three foxes managed to enter the Park and caused several known fatalities among the peafowl population (Petrie 1992b)*.

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* Over the entire breeding season of 1993, only three chicks are known to have fledged at Whipsnade (T. Halliday, pers. comm.).

2.4.2 Identification of chicks

Chicks proved increasingly difficult to capture as their wing feathers developed, and I therefore aimed to catch chicks for marking within the first week or so after hatching. Every effort was made to catch complete broods at one attempt, in order to avoid the female taking

any uncaptured chicks away with her and thus dividing the brood; when this proved impossible, the female and her remaining brood were monitored and the chicks returned directly to the brood. When a complete brood was captured, the attendant hen generally remained within earshot of her chicks while they were being marked, often calling for them with loud "honks" and sharp "kok-kok" calls. If it appeared that she was moving away (for example if the chicks were silent in the bags), she could often be summoned back by my crude imitation of a chick's "peep" distress call (see Chapter Six). Occasionally more than one brood was caught simultaneously, in which case probable siblings and dams were identified from previous and subsequent associations.

Chicks were caught by hand and placed individually into labelled cotton drawstring bags, then weighed using a Pesola 300g balance. Some chicks defaecated while in the bag, but the weight of faeces did not exceed 1-2g. I measured a range of variables on each chick, as outlined in Table 2.2; tarsus, wing and crest length were measured as shown in Figure 2.2. Some chicks, those with a *Pavo cristatus* mut. *nigripennis* parent, possessed white primary feathers, and there was considerable variation in the number and distribution of these feathers (Plates 2.6 and 2.8). Records were therefore made of the plumage characteristics of each chick (Table 2.3). I also took 3 x 4µl blood from a superficial brachial vein (Plate 2.7) for subsequent DNA analysis by Olivier Hanotte and Terry Burke at Leicester University. To date the results of this genetic fingerprinting are not available for inclusion in this thesis, but it is hoped that in the future they will provide an insight into multiple paternity and intra-specific nest parasitism.

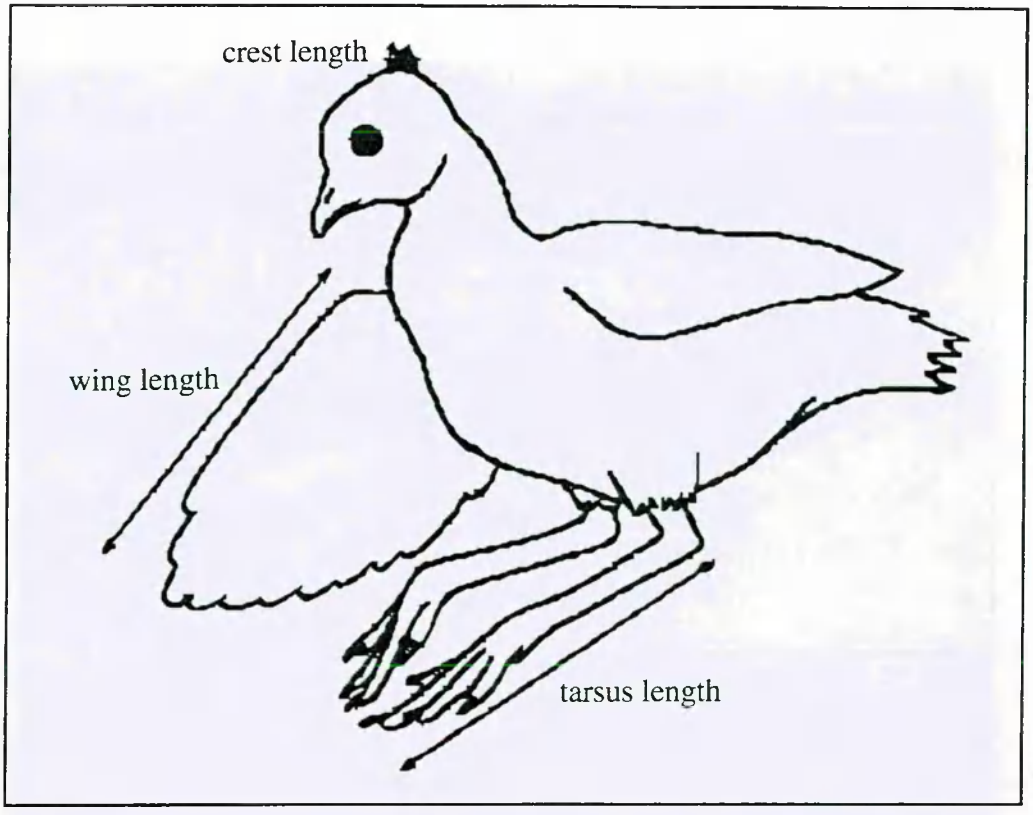


Figure 2.2. Morphological measurements taken on chicks at Whipsnade.

Plate 2.6. Peachick SDG 68 with large number of white primary feathers.

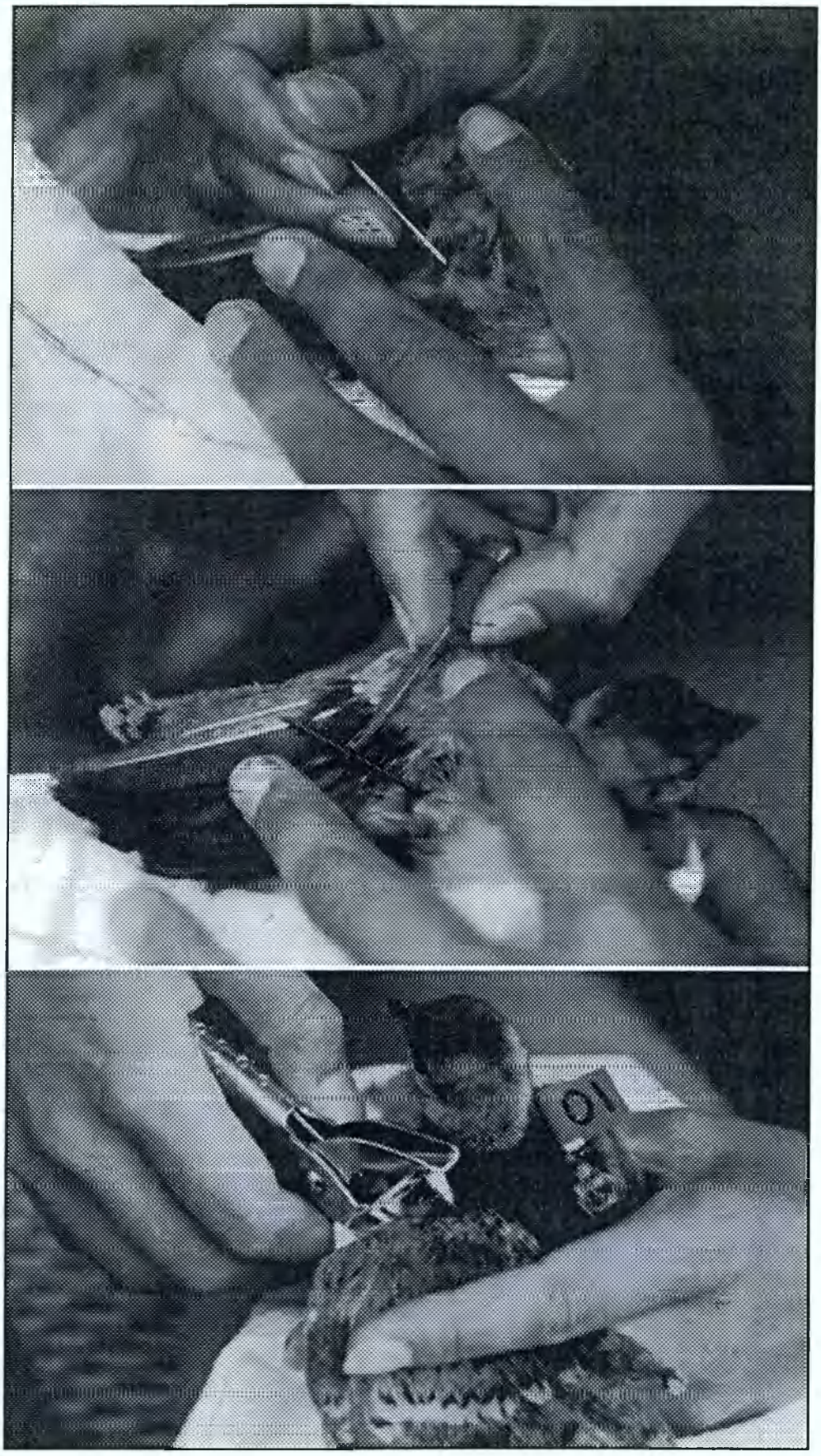


Plate 2.7. Extraction of blood for subsequent DNA analysis, and chick marking. *a:* A 0.8mm bore needle was used to puncture a superficial brachial vein. *b:* The resulting droplet of blood was drawn out into three 4µm capillary tubes, which were then placed in buffer solution. *c:* Metal patagial tags were applied to the chick's wings (see Plate 2.8).

Chick tagged	ODB27 (35C610/611)	Egg tooth	None
Caught with	–O25 (brown; 35C607)	Crest	2.9 mm (one feather)
Broodmates not caught	None	Weight chick + bag	189 g
Female with brood	Red/Green	Weight bag	49 g
Date of capture	16.7.89 (0945)	Weight chick	140 g
Age of chick	22/23 days	Length tarsus to toe	73.9 mm
Site of capture	Flint Pit water corner	Length tarsus to claw	78.0 mm
Plumage (white/brown)	Pale brown	Length wing	125.0 mm
White primaries	None	Blood taken	3.0 cap. tubes
Notes	Female RG had nest N, 6 eggs; 5 chicks hatched 24/25.6.89 (all 5 brown). 30.6.89: RG had two brown chicks, caught 16.7.89. RG with females A20 and B00 (1 brown chick each); all 4 chicks caught together. A20's chick tagged –Y26, B00's chick tagged YDB14. RG more defensive than A20 or B00, which flew off, leaving RG to defend all 4 chicks. Chick ODB27 could fly a little, 20-30m low over the ground. All 4 chicks collected by females in FPP after marking; all seen 1720 in FPP with original parents.		

Table 2.2. Example of data sheet for chicks marked at Whipsnade.

Peachicks were individually marked using metal patagial tags with coloured and numbered plastic tags attached (Plates 2.7 and 2.8), and the age of each chick estimated from size, plumage and overall development. Wenke (1989) suggested a method for sexing the chicks of pheasant species, which involves suspending the animal by its feet and noting whether it curls its body up (female) or hangs straight down (male). This method proved rather less than useful in my study, however, since every peachick I suspended curled backwards! (Plate 2.9). I was therefore unable to reliably sex chicks until they reached three or four months old, when males started to develop barred wing and back feathers and copper primaries, while young females remained a soft brown with darker primary feathers.

Plate 2.8. Individually marked peachick SY 66. Numbered metal patagial tags were applied permanently to the patagium of each wing (the triangular flap of thin skin between humerus and radius), taking care to avoid blood vessels. Each metal tag had a coloured and indelibly numbered plastic tag stapled to it; chicks were numbered sequentially as they were caught, and the combination of colours was unique to each chick. *N.B.* The white primary feathers possessed by this chick differ from those of chick SDG 68, Plate 2.6.

Plate 2.9. An (unsuccessful) attempt to determine the sex of a young peachick. Males were predicted to hang straight down, females to curl their body up; peachicks at Whipsnade however all curled their heads backward.

2.5 Behavioural observations

2.5.1 Equipment

Most behavioural observations were carried out using a pair of Zeiss 8x30 binoculars and an Opticron telescope with 20-60x zoom lens. Photographs were taken with a Pentax P30 camera, plus a 28-80mm Takumar zoom lens or 300mm Tokina lens. An Opticron telescopic tripod and car window mount were used to facilitate observations around the Park; focal watches were performed either from a car, or more usually from a Jamie Wood "Fensman" portable hide.

Time budget analysis required accurate minute by minute observations on focal individuals, and for this purpose a variable timer/bleeper with earpiece was constructed from a diagram in Martin & Bateson (1986) by the Technology Workshop at the Open University. For the

playback experiment described in Chapter Six, recordings of chick calls were made using a Uher reel-to-reel tape recorder with external microphone. The tape was then made into a continuous loop and re-recorded onto high quality cassettes, to provide several minutes of continuous calls. The use of several cassettes prevented distortion of the playback through degradation. Calls were played back using a speaker and long cable.

The equipment described above was used throughout this project; additional equipment specific to particular studies will be described in the relevant chapters.

2.5.2 Techniques

Home ranges, associations and daily routines

The home ranges of individual birds were investigated by thorough fortnightly surveys over the entire Park, as outlined in Section 2.2.1. In addition, these surveys gave an indication not only of the associations between particular adults, but also of the duration of parental attendance, and sex differences in juvenile dispersal. Daily routines of peafowl at Whipsnade were ascertained by observing focal individuals throughout an entire day, recording their location and behaviour at fifteen minute intervals. I was thus able to monitor differences between males and females, and changes in behaviour over the season; the results are outlined in Section 2.2.1.

Time budgets

In order to investigate differences in parental expenditure between females, accurate measures were required of the allocation of resources, including time. Time budgets were used as an indication of investment in nesting (Chapter Three) and brooding (Chapter Five). The choice of focal animal was based on both the category of data required (*e.g.* "hen in last stages of incubation" or "hen with four chicks"), and the accessibility and visibility of the female. The problems and advantages of repeated observations on the same individual will be discussed where relevant in Chapters Three and Five.

For time budget analysis observations were made from either a hide or a car, whichever was more practicable. In each case I was in position for at least 15-30 minutes before starting to

record the subject's behaviour; this appeared to provide the birds with ample time to become accustomed to my (hidden) presence. I used a point-sampling technique at one-minute intervals, and allocated the observed behaviour pattern to one of several pre-determined, mutually exclusive categories. Where two females were visible simultaneously it proved possible to record both of their behaviour patterns, using alternate 30 second intervals, and thereby increase sample sizes. Time budgets were recorded for at least 30 continuous minutes on each individual, and observations from periods shorter than this were discarded. Different categories of subjects and behaviour patterns were chosen for nesting and brooding females, and these will be described in detail in Chapters Three and Five.

Brood defence

Parental investment in chicks can be expressed not only by the allocation of time to parental behaviour patterns, but also by expenditure on brood defence. I aimed to measure the defence behaviour of hens at Whipsnade by recording their response to potential danger, according to the following procedure. Each subject was categorised depending on the number and age of her chicks, and whether or not she was alone or was part of a group. Prior to starting the experiment I observed the behaviour of the focal animal for fifteen minutes, both to ascertain that she was not behaving abnormally, and that if she was aware of my presence she was not apparently disturbed by it. I then acted as a potential predator by walking steadily towards the hen and her brood, and noted both her general behaviour and the minimum distance she would allow me to approach before fleeing and abandoning her young. This experiment is described in greater detail in Chapter Four.

Playbacks

The phenomenon of post-hatch brood amalgamation in the Whipsnade population is discussed in Chapter Six, and Section 6.3 is concerned with an experimental attempt to discover how such a strategy may have arisen. For this experiment I recorded the "peeping" distress calls of several chicks in the hand in 1989, aged between four days and five weeks. My initial pilot study in that year showed no significant difference in the responses of females to the calls of different aged chicks, in spite of a slight lowering in pitch with

increasing age. Throughout the subsequent experiment I therefore used the call of a single chick, aged five days old.

Minute by minute time budgets of focal females were sampled for fifteen minutes before experimentation, as above. The chick call was then played for one minute, at a volume as close as possible to that of live peachicks (as perceived by the human ear). The behaviour of the focal hen was recorded at five second intervals throughout that minute, and for the following five minutes. The playback was then repeated for a further minute, and observations continued for the next five minutes.

The six categories of female used in this study included hens on the nest and hens with and without chicks, and the responses of each class will be discussed in detail in Chapter Six.

Analyses

The majority of statistical analyses performed on the data are non-parametric, since such tests are more robust and make fewer assumptions than parametric tests, and are therefore more suitable for non-normal data. The specific test used for each analysis in the thesis is identified individually. Analyses are performed according to the protocols described in Siegel (1956), either by hand or using the computer packages Microsoft Excel 4.0, StatView 512+™ 1.0, StatWorks™ 1.2 or CA-Cricket Graph III 1.0.

The α significance level used throughout this thesis is 0.05, and wherever possible exact probabilities are given. The criteria for using one- or two-tailed tests is as follows: where specific uni-directional predictions are made (*i.e.* A is predicted to be greater than B), a one-tailed test is used; otherwise a two-tailed test is used. Many of the relationships between variables are shown graphically, with lines depicting the regression or correlation between the two variables. The program CA-Cricket Graph III was used to draw the graphs and inserted the required lines automatically.

CHAPTER THREE
PARENTAL INVESTMENT IN NESTING

3.1 Introduction

3.1.1 Parental investment in nesting

Some of the variety of modes of parental care have been introduced in Chapter One. In birds, these include several forms associated with nesting and incubation behaviour, such as nest preparation, the formation of large, heavily yolked eggs, the carrying of those eggs, incubation (which may require the formation of a brood patch), and nest defence. In some cases the costs of these activities can be substantial; for example, the daily costs of egg production across a range of bird species have been estimated at 29-35% of the basal metabolic rate (BMR) of the laying hen, whose protein requirements increase by 86-230% (Robbins 1983; Wootton 1979; Hinton 1981; Clutton-Brock 1991). Similarly, the cost of maintaining egg temperature has been evaluated at 10-30% BMR in passerines (King 1973), but 30-40% BMR in petrels (Croxall 1982) . Such variation can arise through differences in the surface area to volume ratio, the ambient nest temperature, and the decrease in time available for the sitting parent to feed.

The degree of parental care shown to offspring varies widely between different families of birds, from the megapodes, which lay their eggs in mounds of rotting vegetation and hence do not even incubate them, to some seabird species, which may continue to care for the juveniles for many months, thereby being able to breed only every other year. Similarly, the percentage weight of eggs occupied by the yolk ranges from around 15% in the gannets and boobies to over 60% in the kiwis (Carey *et al.* 1980). The size of the egg also varies relative to the parent's body size: for example, a kiwi weighs less than 2kg, yet lays a single egg weighing 350-400g; at the other extreme are many species (*e.g.* most fish) which produce huge numbers of tiny offspring (Stearns 1992). With regard to peafowl, Johnsgard (1986) describes each egg as representing 3-6%, and the whole clutch 15-50%, of the

female's body weight; the modal clutch size is given as 4-6, and mean egg size as 69-75mm x 52-54mm, weighing 100-104g (Baker 1930; Sharma 1972; Ali & Ripley 1983).

Whatever the absolute level of parental investment, the resources available to parents for investment can be allocated proportionally in many different ways. In multiparous species, this applies to the division of resources not only within a particular breeding attempt, but also over the individual's expected lifespan. For example, with regard to the level of parental expenditure on a clutch, there is a whole series of parental options, including:

- whether to provide any parental investment at all, beyond the production of gametes;
- when and where to lay the eggs (this may depend upon the date of copulation, nest site availability *etc.*);
- how large to make the eggs, and how much yolk to provide;
- how many eggs to lay;
- for how long to incubate the clutch;
- how well to protect the clutch (*e.g.* through nest defence, vigilance for predators *etc.*).

Some of these "decisions" apply to both males and females (*e.g.* whether to care at all), whereas others are necessarily restricted to females (*e.g.* propagule size).

The concept of the reproductive value of an individual, of a certain age and sex, was introduced in Chapter One: Williams (1966b) defined residual reproductive value as "the mean amount of future reproductive success for individuals of that age and sex in the population" (see also Fisher 1930; Stearns 1992). Reproductive value is thus strictly a characteristic of age classes and not of individuals, but an individual's value may be estimated from the reproductive value of its age class (Stearns 1992), and it should invest in accordance with its *expected probabilities* of reproductive success and survival. If this second, looser definition is applied, one can predict changes in an individual's reproductive value over its lifespan. The reproductive value of most animals increases to the age of peak productivity (normally when the organism reaches maturity), and then declines until death, but is also obviously dependent upon the population growth rate (Stearns 1992).

Parental investment can be considered in terms of the reproductive value of both parent and offspring. The value of an offspring will increase with age, since less parental expenditure is required for the offspring to attain independence. However, the residual reproductive value of a parent declines with age, as the number of opportunities remaining for breeding decreases throughout the animal's lifetime. In addition, the fitness of both individual offspring and parents is likely to increase with increasing quality, since higher quality individuals are more likely to mate and breed successfully and produce higher quality offspring; but may decrease with breeding experience, if parental expenditure in a brood lowers the parent's subsequent reproductive success (Williams 1966a,b; Pianka 1976; Dawkins & Carlisle 1986; Winkler 1987; Curio 1988; Montgomerie & Weatherhead 1988).

Parents would be expected to adjust their levels of parental expenditure in relation to variation in its benefits to the offspring, and in its costs to themselves, in order to maximise their own fitness (Winkler 1987). Thus parental care should vary according to both the parent's own residual reproductive value and their offspring's reproductive value, as well as in relation to environmental factors.

For example, variables determining the reproductive value or fitness of a clutch include:

- degree of parent-offspring relatedness;
- egg size;
- clutch size;
- egg quality;
- age of eggs.

Similarly, variables determining the parent's own fitness or reproductive value include:

- parental age;
- parental breeding experience;
- parental quality.

Environmental factors will also play a role in determining the level of parental expenditure in a clutch, and these include:

- resource availability;

- time in breeding season, *i.e.* whether there would be an opportunity to nest again if the current breeding attempt is unsuccessful;
- level of nest predation;
- level of inter- and intraspecific nest parasitism;
- expected level of juvenile competition;
- expected harshness of the juvenile environment.

Once the level of parental expenditure for a particular breeding attempt has been set, selection will act upon the relative allocation of resources within that nesting attempt. One important way of dividing such resources is to determine (i) how large the eggs should be, and (ii) how many eggs to lay. It has often been assumed that there is a trade-off between egg size and number (*e.g.* Lack 1968; Lloyd 1987). Smith & Fretwell (1974) proposed a model for this trade-off (Figure 3.1), which describes the suggested relationship between parental expenditure and the fitness of individual offspring. They hypothesise that offspring fitness will not increase at all until a certain level of parental expenditure has been reached, and then will increase according to the curve shown in Figure 3.1. The optimum level of expenditure occurs at point B, where a straight line from the origin lies tangentially to the curve. Both the levels of parental effort represented by points A and C will produce lower parental fitness than the optimum.

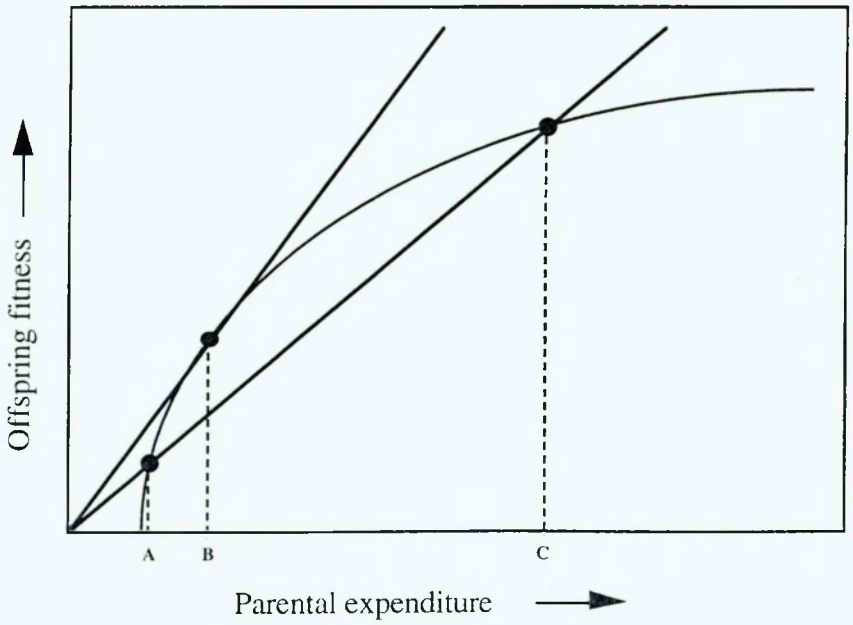


Figure 3.1. Smith & Fretwell's (1974) model for the trade-off between offspring size and number. The curve represents the relationship between the fitness of individual offspring, and parental expenditure per offspring. For explanation, see text.

It has however been subsequently pointed out that Smith & Fretwell's model may be rather simplistic (see Section 1.3.1). For example, if the shape of the fitness curve is linear or exponential, a line drawn through the origin will always meet the curve at its maximum point, and the optimum number of offspring will be one (Clutton-Brock 1991). In such cases offspring size will often be correlated with parental size (Stearns 1976; Winkler & Wallin 1987; Partridge & Harvey 1988). Alternatively, there may be several optima for the level of parental expenditure, for instance where the optimum propagule size differs for parents of varying quality (Clutton-Brock 1991).

The simple trade-off model above can be refined by taking into account additional variation in other factors, including environmental quality (*e.g.* Bagenal 1969; Vance 1973a,b; Fraser 1980; Lloyd 1984), parental resource availability (*e.g.* Lack 1968), offspring quality (*e.g.* Boersma 1982), parental ability (*e.g.* Sargent *et al.* 1987), selection on clutch size (*e.g.* McGinley & Charnov 1988; McGinley 1989), juvenile mortality (*e.g.* Sibly & Calow 1986; Sargent *et al.* 1987), and the division of resources between offspring (*e.g.* Lack 1947; Slagsvold *et al.* 1984). In addition, it is not uncommon for egg size and clutch size to be positively correlated, since a parent's total reproductive effort determines both propagule size and number; consequently an increase in parental effort could increase both variables, and both are likely to affect offspring fitness (Clutton-Brock 1991).

Optimal egg size is likely to be affected by a complex combination of selection pressures and constraints, and by the influence of egg size both on the duration of subsequent stages of juvenile development and on the instantaneous rate of juvenile mortality. The following are a number of possible factors which may operate directly or indirectly on the size of propagules.

- *Access of the female to resources.* The ability of a female to manufacture eggs will depend in part upon the availability of nutrients (*e.g.* protein and fat for the yolk and albumen) and other materials (*e.g.* calcium and grit for the shell); any limitation in these resources may thus constrain egg size (Welty & Baptista 1988).

- *Environmental quality.* In a range of species, a deterioration in environmental conditions results in increased egg size and decreased clutch size (Lack 1947; Bagenal 1969). For example, ground nesting birds often have larger eggs than cliff or tree nesters, since they may be exposed to greater environmental stresses, such as temperature variation (Nice 1962; Lack 1968). Many birds also start to incubate the clutch as soon as the first egg is laid, resulting in asynchronous hatching and chicks of different sizes within a brood (*e.g.* the cattle egret *Bubulcus ibis*; Fujioka 1985). This would facilitate brood reduction through the death of the youngest and smallest chick(s) in times of extreme hardship, thereby permitting the survival of the remaining chicks (Lack 1947; O'Connor 1978; Hahn 1981; Fujioka 1985; Mock & Ploger 1987; Boersma & Stokes 1991). There is however no evidence that parents are actively discriminating against smaller chicks (Spellerberg 1971; Mock 1984), although neglect of the terminal egg in a clutch may be part of an adaptive parental brood reduction strategy (Evans & Lee 1991).

  Similar strategies are adopted by species which lay eggs of decreasing sizes within a single clutch, facilitating the demise of later-laid chicks if conditions dictate, including the shag *Phalacrocorax aristotelis* (Stokland & Amundsen 1988), the herring gull *Larus argentatus* (Parsons 1976), and a range of other species, particularly large, altricial, and open-nesting ones (Slagsvold *et al.* 1984).

- *Predictability of the hatched young's environment.* If juvenile resources tend to be patchily distributed in time or space, young which are more highly developed on hatching may be better able to survive periods without nourishment than more altricial young (Boersma 1982; O'Connor 1984). An increase in egg size (or quality) might therefore be a strategy by which parents equip their offspring for such conditions. For example, many seabirds lay only one or two large eggs, since food is limited and often unpredictable (Boersma 1991; Bright 1993). An extremely unpredictable or heterogeneous environment may also give rise to an optimal *range* of egg size, rather than a single optimum (Capinera 1979; Crump 1981; Philipi & Seger 1989).

- *Intra- and interspecific competition.* The production of large eggs can give rise to large offspring, which may fare better in competitive situations (*e.g.* at feeding sites) than those

from smaller eggs. Such competitive advantages can persist for much longer than the duration of the chick stage; early growth has often been shown to affect subsequent reproductive success, with larger juveniles being more successful as adults in territory acquisition and mating success, for example (Clutton-Brock 1991).

- *Selection pressures operating directly on clutch size* can indirectly affect egg size. If offspring fitness is almost entirely determined by clutch size, then this will remain fairly constant at some optimum size throughout the population, and differential investment between individuals will be expressed as variation in egg size. For example, if a parent can only incubate a single egg, or if it can only care for a single offspring, the majority of the population will produce a uniform clutch size of one, and egg size will vary. Similarly if evolution selects for a large clutch (or brood) size, for example because it is more likely to satiate predators, then clutch size will be consistently high within the population and egg size will vary between individuals.

- *Female body size.* If clutch size is relatively fixed, as discussed above, then egg size might be expected to vary in proportion to the mother's body size. Propagule size has been found to be related to the female body size in many mammals and birds (Clutton-Brock 1988) which could suggest that the female's pelvis size acts as a constraint on egg or neonate size. This raises the question, however, of why animals have not simply evolved larger pelvises (Clutton-Brock 1991). In addition, the body size *versus* propagule size relationship is often negatively allometric (*i.e.* as body size increases, eggs are equivalent to a lower proportion of the female's body weight) (Welty & Baptista 1988). The problem of the influence of body size on egg size is a thorny one, since both adaptations and constraints are necessarily involved. It is only possible to discover the effects of environmental factors if body size is held constant, which poses its own problems (Clutton-Brock 1991).

- *Predation.* Since the average incubation period of birds increases with egg weight, larger eggs take longer to incubate. Rahn & Ar (1974) give the formula: [incubation in days] = 12.03[egg weight in grams]$^{0.217}$ (see also Steele 1977; Welty & Baptista 1988). If there is considerable danger of the female being predated while on the

nest, shorter incubation periods may be selected for, which implies the production of smaller eggs. There is also some evidence that larger clutches take longer to incubate. For example, in his experimental study of the blue tit *Parus caeruleus*, Smith (1989) found that the disadvantages of longer incubation (*e.g.* longer exposure to nest predators, increased risk of egg chilling, decreasing fledgling survival over the season) were minimised by greater energy expenditure by the parents.

- *"Safe harbor"*. The length of incubation can depend not only on the risk of predation to the sitting parent, but also on the probability of mortality for the clutch. Natural selection should favour spending as little time as possible in life history stages which confer very low survivorship (Williams 1966a); the relative mortality rates of eggs and juveniles can thus determine the duration of each developmental stage. This hypothesis is supported by the findings of Shine (1978), who reviewed propagule size and parental care in a range of poikilothermic groups, and found that "species that protect their offspring usually produce larger (and hence fewer) propagules than do related species that do not protect their offspring". He termed this the "Safe Harbor" model - *i.e.* if the survival of eggs is higher than that of juveniles, for example through the existence of parental care, then the egg stage can be regarded as a "safe harbour". The assumptions implicit in Shine's original model are not necessarily justifiable - for example, he assumes juvenile survival to be independent of egg size, but as pointed out above, offspring fitness is frequently enhanced by increasing egg size. Subsequent models have therefore incorporated this relationship (Sargent *et al.* 1987; Shine 1989).

- *Juvenile mortality rate.* The instantaneous mortality rate of juveniles can itself be affected by egg size; if larger or more precocial offspring are less likely to die (*e.g.* from exposure or predation) than smaller ones, then selection may give rise to larger eggs (for the reasons outlined under *competitive advantage*, above).

Relative investment in a nesting attempt can be measured not only in terms of the physical resources allocated to eggs (*e.g.* egg size, clutch size, percentage yolk per egg *etc.*), but also with behavioural correlates, such as nest defence or egg rolling behaviour. The costs of such behaviour patterns to an incubating parent (and, indeed, the benefits for the offspring)

are considerably more difficult to measure than, for example, the energy required to lay eggs or clutches of different sizes. In many field studies it is only possible to attempt comparative studies, looking at variation in behaviour patterns such as nest defence between parents with different sized clutches; consequently predictions are often qualitative rather than quantitative.

Behaviour patterns displayed by incubating individuals can only be regarded as "parental" if they contribute directly to the fitness of the clutch, and thus indirectly to their own inclusive fitness, at some direct cost to themselves. Certain observed behaviour patterns, such as vigilance, may benefit the clutch, through the early detection and discouragement of predators and nest parasites, for example; or benefit may be gained directly by the sitting adult, or indeed both clutch and parent. Other patterns, such as nest defence or egg rolling, are much easier to assign to the category of parental behaviour, since they obviously benefit the clutch directly. In order to determine whether a behaviour pattern is truly parental, one can for example compare the level of that pattern displayed by incubating and non-incubating (sitting) adults; in addition, if there is an increase in the level of that behaviour with increased clutch size, it is reasonable to assume that there is at least some parental element to the behaviour pattern.

Some nesting behaviour patterns which may be considered to contribute directly to offspring fitness include:

- *Nest construction and maintenance.* Birds' nests can be elaborate affairs, such as the hanging woven nests constructed by the weaver birds, or they can be merely a scrape on the ground, as displayed by the pheasants; they may be lined, for example with feathers or grass, or completely bare (Welty & Baptista 1988). In any case, nest preparation and maintenance is generally necessary for protection of the clutch, from predators, parasites, extremes of temperature, or simply to prevent the eggs rolling away, and as such may be regarded as parental investment.

- *Nest attendance.* There is enormous diversity in the incubation patterns of birds: Skutch (1957) classified 160 families, and found that in 54% of them both sexes are responsible

for incubation; the female is solely responsible in 25%; the male alone in 6%; and in the remaining 15% the clutch may be incubated by the male, female, or both sexes. Even when both sexes perform incubation duties, the female is often primarily responsible and the male feeds her at the nest. This variety of incubation patterns produces some differences in the modes of nest attendance (*i.e.* the proportion of time that the clutch is actually being incubated by the parent).

Some species demonstrate 100% nest attendance throughout incubation; the parent is never absent from the nest and is fed at regular intervals by its mate (for example in the hornbills (fam. Bucerotidae), the female is "imprisoned" on the nest by the male, which blocks the entrance hole with mud, and supplies both her and the chicks with food). In other species with biparental care (*e.g.* many passerines: Kendeigh 1952; Lack 1968), both parents are responsible for incubation of the clutch, and nest attendance is also 100% as the parents leave the nest only when relieved by their mate.

For species with uniparental care, however (*e.g.* the pheasants, fam. Phasianidae), it is not possible to have continuous attendance at the nest, since the incubating parent has to leave the nest from time to time in order to feed. While a parent is absent from the nest, its clutch is at increased risk of predation, parasitism, heating or cooling, and the eggs are receiving no direct parental care from the adult. The parent is contributing only indirectly to the fitness of its offspring, by ensuring that the clutch will have a healthy parent to incubate, protect and care for it; for example, a starved parent may be unable to adequately defend a nest against predators. In these species, therefore, the proportion of time that the parent spends at the nest can provide an indication of relative levels of parental expenditure.

- *Egg turning.* Regular turning of incubated eggs is essential for the development of the embryo, to provide even temperatures throughout the egg, to stimulate the growth of blood vessels, and to prevent the embryonic membrane adhering to the inside of the shell (Skutch 1976; Welty & Baptista 1988; Deeming 1991). As the egg is rotated, the embryo remains uppermost, but once the egg starts to "pip" (*i.e.* the egg tooth of the chick begins to break through the shell) it is no longer turned. There is wide variation in the frequency

of egg-turning: for example, the redstart *Phoenicurus phoenicurus* turns its eggs once every eight minutes, whereas the ring-necked pheasant *Phasianus colchicus* does so only once an hour (Welty & Baptista 1988). Egg turning behaviour thus contributes directly to offspring fitness, by maintaining the development of the embryo, and as such may be regarded as an expression of parental expenditure.

- *Nest defence.* Incubating parents can increase the likelihood of their offspring surviving to maturity by defending the clutch against potential predators and inter- and intraspecific nest parasites. Sometimes the mere presence of an adult at a nest will be sufficient to deter intruders; on other occasions an active display of aggression is necessary to prevent the clutch either being attacked and consumed, or its fitness being lowered by the addition of a parasitic egg.

The intensity of nest defence behaviour can therefore be regarded as a measure of parental investment, since it contributes directly to the offspring's fitness at some cost to the parent. Determination of the costs of defence behaviour is exceedingly complex, since there is not only a metabolic cost involved, but also a considerable cost in terms of the risk to the parent; once again, it is often only possible to investigate the behaviour through comparative studies. Thornhill (1989) produced a neat comparison of nest defence in red junglefowl (*Gallus gallus spadiceus*) in relation to parental and offspring reproductive value. He experimentally manipulated the reproductive value of the offspring (using eggs and chicks of different ages), while simultaneously controlling for variation in the age and nesting experience of the female; his results are discussed in Section 4.1.1. Such experiments are invaluable for an improved understanding of the role of nest defence in parental investment, but are more difficult to perform in the field.

It is important to remember, however, that the clutch will gain nothing if the parent "fights to the death" (in the majority of cases, this would result in the offspring perishing without adequate incubation and care); whereas if the parent is forced to desert the clutch in the face of a predator, he or she may still survive to breed again, thereby contributing to the inclusive fitness of the abandoned clutch.

- *Vigilance*. Vigilance (defined as the probability of stimulus detection (Mackworth 1970; Dimond & Lazarus 1974; Lendrem 1982; Lazarus 1990)) is notoriously difficult to study, since it is not always possible to determine (a) whether the observed behaviour pattern actually has the function of increased vigilance, and (b) what the animal is being vigilant for. It is therefore usually necessary to take a likely behaviour pattern and observe whether it varies according to pre-defined expectations of what the animal is looking for. One such potential candidate for "vigilance" is scanning behaviour, in which an individual raises its head at intervals and looks around the horizon (*e.g.* Inglis & Lazarus 1981; Dehn 1990). In this way it may well be looking out for predators, but scanning may also have the purpose of detecting possible mates, competitors, parasites, or even food patches. The behaviour pattern is generally easily identifiable and can be measured in several ways, including total time spent in a vigilant posture, scanning bout duration, duration of the intervals between bouts, and regularity or randomness of bouts.

In addition, there is the problem of how to determine whether an animal has detected whatever it is looking for or not. One could measure the response of the animal to the stimulus, but not only does this include detection time plus the delay between detection and response, but it also does not take into account those occasions on which an individual detects the stimulus but decides not to respond (Lazarus 1990). There is also little conclusive evidence that a vigilant posture actually increases the chances of detecting a predator, although Fitzgibbon (1989) showed that a cheetah, *Acinonyx jubatus*, preying on a herd of Thomson's gazelles, *Gazella thomsoni*, is significantly more likely to stalk and attack those that are less watchful.

In order to discover whether vigilance is an example of parental behaviour, the relative levels of vigilance can be compared between parents and non-parents in similar situations (*e.g.* sitting *vs.* incubating; walking with *vs.* without chicks *etc.*). Although there have been a large number of studies of vigilant behaviour, the majority have concentrated on its frequency in grouped versus solitary animals (*e.g.* Jennings & Evans 1980; Inglis & Lazarus 1981; Dehn 1990; see also Chapters Four and Five). Any investigation of vigilance during incubation has to adopt a different approach, however, since incubating

adults are necessarily either clustered or solitary (usually the latter) throughout the whole incubation period, and their behaviour in each situation cannot therefore be compared. Nevertheless, if scanning behaviour can be proved to have a "parental" element, it can provide a useful indication of changes in parental expenditure over time, and can be compared between parents with clutches of various sizes.

As discussed in Section 1.3.3, it is possible to classify an act of parental care as "shared" or "unshared", according to the nature of the behaviour and its relationship with clutch or brood size (Lazarus & Inglis 1978, 1986; see also Altmann *et al.* 1977 and Wittenberger 1979). Behaviour patterns are not necessarily restricted to one category or the other - for example, certain parental acts may be shared in some circumstances and unshared in others.

Where there is a certain minimum level of investment necessary for offspring survival, shared components of parental investment are expected to increase with clutch or brood size; unshared parental investment might be assumed to be independent of the number of offspring (Lazarus & Inglis 1986; Montgomerie & Weatherhead 1988). However, for unshared anti-predator behaviour patterns, investment is predicted to increase with brood size if predators typically take the whole brood ("brood loss"), and to be independent of brood size if they take single offspring ("fixed loss") (Lazarus & Inglis 1986).

With regard to the behaviour of incubating parents, the benefits of some behaviour patterns (*e.g.* egg turning) may be considered to be shared, while others (*e.g.* vigilance) might be unshared. The act of actually incubating the eggs (*i.e.* providing the warmth necessary for development of the embryo) could be shared or unshared, depending upon whether the size of the brood patch, position of the egg in the nest *etc.*, affects the amount of warmth received by each egg.

3.1.2 Nesting at Whipsnade

The discussion above demonstrates that parental investment in nesting can be examined in both material and behavioural terms, and related to factors such as parental and offspring reproductive value and environmental conditions. The nesting behaviour of peahens at Whipsnade was thus investigated with regard to the amount of material resources that were

allocated to the production of a clutch (*i.e.* the size and number of eggs), and behavioural expenditure on that clutch (*i.e.* nest location, egg turning, nest defence and vigilance). These observations could then be related to the residual reproductive value of the hen (*i.e.* her age, condition and breeding experience), and to the reproductive value of her clutch (*i.e.* size and number of eggs, and time since the start of incubation). It should however be noted that it was not always possible to collect reliable data on some of these parameters; for example, the condition of the incubating female could never be measured directly, and indirect evidence was only available through previous capture records (which could be up to five years old). These problems are discussed individually in Section 3.2.

The aim of this chapter is therefore to address the following questions, with predictions according to current reproductive effort theory:

- Which factors are important in determining the *material* parental investment in eggs?

  According to reproductive effort theory, parental expenditure on clutch size and/or egg size should increase with decreasing parental residual reproductive value. Thus one might expect older or more experienced hens to produce larger eggs and/or clutches than younger ones. Additional factors which may influence egg and clutch size include date in breeding season, whether the female has previously attempted to breed in that season, climate, food availability, vegetative nest cover, predation levels *etc.*

  For example, if a hen has a limited level of resources available for reproduction within a particular year, the production of one clutch may influence the resources available for subsequent clutches. This may be reflected by declining clutch and/or egg sizes in progressive nesting attempts.

  In contrast, if environmental conditions deteriorate over the season, selection may favour an increase in propagule size (which may lead in turn to smaller clutches if there is a life history trade-off). If vegetative cover declines, and/or the risk of nest predation increases, later clutches may be smaller in order to reduce the length of incubation (see Smith 1989).

- Which factors are important in determining the *behavioural* parental investment in eggs?

Reproductive effort theory predicts that peahens should expend greater parental care on offspring with greater reproductive value, and parental expenditure should increase with declining parental residual reproductive value. In behavioural terms, one might therefore expect, for example, higher levels of nest attendance and vigilance by older females, those with large clutches and those with clutches in the later stages of incubation.

Environmental factors which may influence the nesting behaviour of peahens include many of those listed above; for example, a decrease in vegetative nest cover over the season may result in increased vigilance by peahens (however, hens may be more watchful since not only their clutch but they themselves are more exposed to predators).

The question of what determines the level of parental expenditure on a clutch is considerably more complex than might at first appear. In this chapter, I aim to untangle some of the factors which may influence material or behavioural investment by comparing peahens which are similar as far as possible in every respect apart from the factor being examined. As well as considering such factors (*e.g.* clutch size) in isolation, I have also attempted to investigate interactions between them; for example, a seasonal trend in clutch size may be influenced by variation in predation levels, food availability, nest cover, laying dates of hens of different ages, or other selective pressures on females to invest according to the time of year.

In addition, the behavioural expenditure of peahens is examined in relation to whether the benefits of a particular parental act are expected to be shared or unshared (Lazarus & Inglis 1978, 1986). However, it should be pointed out that the *benefits* of parental investment for the peachicks in the Whipsnade population (*e.g.* variation in growth rates, or subsequent reproductive success) could not be measured directly; instead I have examined parental expenditure by peahens by comparing the behavioural *costs* to parents in various situations.

3.2 Methods

3.2.1 Nests and eggs

The methods used to find and individually identify nests and eggs were described fully in Section 2.3.2. Both incubated and deserted clutches were recorded; a nest was defined as "viable" if it was seen to be incubated at some stage, even if it did not successfully hatch. Non-viable clutches included abandoned single eggs which appeared to have been laid indiscriminately, often in exposed positions with no obvious nest scrape (see Section 3.4.1), and large unattended clutches of up to 20 eggs* which were almost certainly laid by more than one female (see Section 3.4.2). Not all incubated clutches were discovered prior to hatching - I estimate the proportion missed to be between 20% and 35%. Since those nests not discovered are inherently likely to be those which were well concealed, in inaccessible areas of the Park, and with high levels of nest attendance, my observations may well be biased towards the more easily discovered nests; nevertheless, comparisons between peahens within this sample should still be valid.

3.2.2 Incubation behaviour

In order to investigate the relationship between parental investment in incubation and the reproductive value of the female or her clutch, it is necessary to determine which particular incubation behaviour patterns are components of parental care. To this end, I compared the behaviour of incubating females with that of non-incubating, sitting hens, and used those behaviour patterns exhibited significantly more frequently by incubating than non-incubating females as manifestations of parental care. These "parental behaviour patterns" can then be examined for variation with respect to differences in parental or offspring reproductive value (Section 3.1).

The reproductive value of a clutch is related to factors such as egg size, clutch size, date of lay and stage of incubation (Section 3.1). Larger eggs often hatch fitter chicks, better able to

* In early June 1993, an unattended clutch of 35 eggs was found at Whipsnade (M. Petrie, pers. comm.).

withstand environmental pressures, and are thus worth more to the parent in terms of their increased probability of surviving to breeding age. Similarly, eggs in the later stages of incubation have less time remaining at risk of nest predation, and require less parental expenditure (*e.g.* in incubation) to reach hatching, and are therefore of higher reproductive value than newly laid eggs. Larger clutches are generally worth more than smaller ones (all other things being equal), since they represent more copies of the parental genome to be passed on to future generations. Clutches which are laid early in the season (in temperate species) have a higher value than later clutches, since chicks hatched from early clutches have more time to grow and develop before the onset of winter, and therefore have increased probability of survival.

The residual reproductive value of an incubating hen declines with her age (Sections 1.3 and 3.1). As with a female's *material* investment in eggs, one might expect females of a lower residual reproductive value to invest more *behaviourally* in a clutch - *i.e.* older hens should expend relatively more time and energy on the care of their eggs than younger females. However, potentially confounding predictions are that older females in better condition, or with more nesting experience, may invest more in incubation than young hens which are light or inexperienced, since the cost of such investment is proportionally less.

I compared the parental components of incubation behaviour between hens of different ages and body condition, and between females with clutches of differing reproductive value, according to the methods described below.

The equipment used for the observation of incubating hens is described in Section 2.5.1, and Section 2.5.2 introduces the use of time budgets for the analysis of incubation behaviour. Pilot observations of nesting females revealed that hens remained on the clutch almost continuously for 24 hours a day. Most females left the nest twice a day to feed, once between 1000 and 1100 hrs, and again between 1500 and 1600 hrs; they were rarely absent from the nest for more than 15-20 minutes at a time. Consequently I decided to use two separate observation periods per observation day on each focal hen, taking account of these feeding times: 0900-1200 hrs, and 1400-1700 hrs.

Focal peahens were selected on the basis of both their accessibility for observation, and their clutch size and stage of incubation. In every case a hide was positioned some distance (minimum 25 metres) from the nest, at least a day in advance of the observation periods; given the general level of disturbance from the public at Whipsnade there was no evidence that the presence of a hide troubled the hens in any way. In one case a female even made her nest within two metres of a regularly-used large hide, in Flint Pit Paddock.

Nesting females were observed at various stages of their incubation period. Additional data recorded from each focal nest included date, clutch size, female age and nesting experience (if known), nest cover, weather, and proximity to potentially disturbing features such as pedestrian walkways *etc.* Time budgets were calculated as described in Section 2.5.2, by allocating each observed behaviour pattern into one of the categories given in Table 3.1. Plates 3.1*a-e* illustrate the five behavioural categories (a) to (e) respectively.

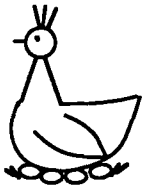
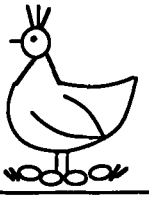
(a) Sitting vigilant (head high, alert, neck feathers often raised) 	(b) Sitting awake (eyes open, but not vigilant) 
(c) Sitting dozing (eyes closed or half closed, head often on neck or under wing) 	(d) Preening 
(e) Turning eggs (standing, rolling eggs with beak) 	(f) Pulling vegetation (using beak to pull grass, leaves *etc.* over back) 
(g) Standing at the nest (not rolling eggs) 	(h) Absent from the nest 

Table 3.1. Categories of behaviour used in time budget analysis of nesting peahens.

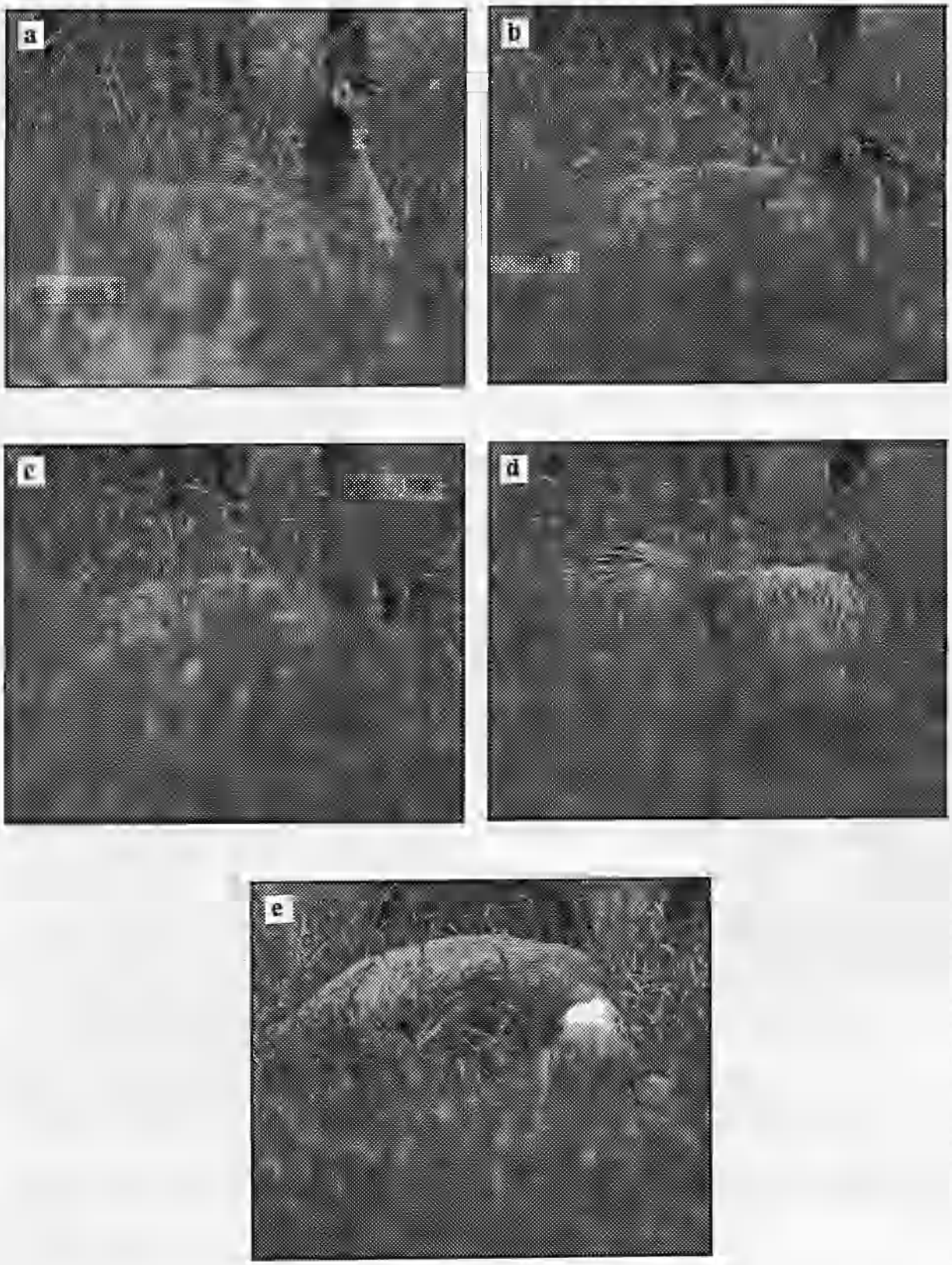


Plate 3.1. Behavioural categories of nesting peahens (see Table 3.1). *a:* Sitting vigilant; *b:* Sitting awake; *c:* Sitting dozing; *d:* Preening; *e:* Turning eggs.

3.3 Results

3.3.1 Nests and eggs

A total of 30 nests (including 21 viable and 9 non-viable) was located prior to hatching in 1989, 50 (including 30 viable and 20 non-viable) in 1990, and 27 (including 11 viable and 16 non-viable) in 1991 (Table 3.2). Over the three years the 45 non-viable nests consisted of 60% single abandoned eggs (see Section 3.4.1), 20% extra-large clutches (Section 3.4.2), and 20% clutches apparently incubated but deserted before discovery.

Annual eggs and nests	Viable nests	Single eggs	Dump nests	Deserted clutches	Annual total
Total nests 1989:	21	7	1	1	n = 30
Total eggs 1989:	91	7	13	2	n = 113
Mean clutch size:	4.33±1.76	1.00±0.00	13.00±0.00	2.00±0.00	3.77 ± 2.70
Total nests 1990:	30	14	3	3	n = 50
Total eggs 1990:	143	14	25	8	n = 190
Mean clutch size:	4.77±1.91	1.00±0.00	8.33±4.04	2.67±0.58	3.80 ± 2.81
Total nests 1991:	10 (+ 1)	6	5	5	n = 26 (+ 1)
Total eggs 1991:	64 (+ ?)	6	69	22	n = 161 (+ ?)
Mean clutch size:	6.40±2.62	1.00±0.00	13.80±4.66	4.40±1.34	6.19 ± 4.92
Grand total nests:	**61**	**27**	**9**	**9**	**n = 106**
Grand total eggs:	**298**	**27**	**107**	**32**	**n = 464**
Mean clutch size:	**4.89±2.33**	**1.00±0.00**	**11.89±4.70**	**3.56±1.42**	**4.38±3.62**

Table 3.2. Clutch sizes and viability of nests in 1989, 1990 and 1991.

The frequency distribution of clutch sizes is shown in Figure 3.2. Overall mean viable clutch size was 4.885; mean non-viable clutch size (all three types) was 3.689, giving the overall mean size of all clutches 4.377.

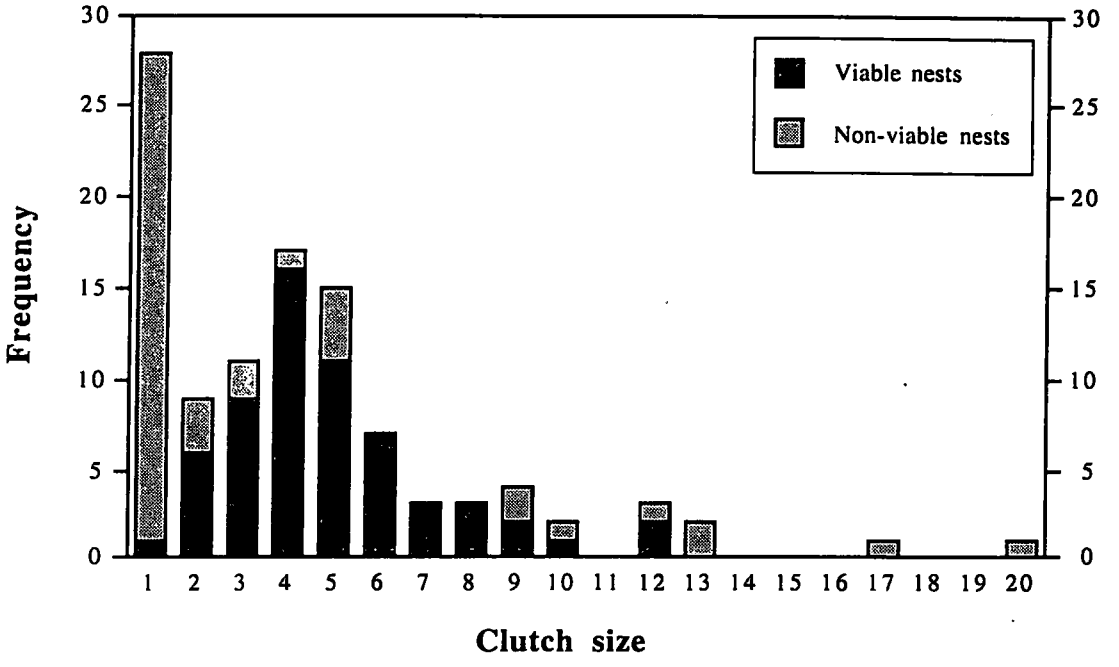


Figure 3.2. Frequency distribution of viable and non-viable clutch sizes; data from 1989, 1990 and 1991 are combined. Overall mean viable clutch size = 4.885 ± 2.327, n = 61; mean non-viable clutch size (all three types) = 3.689 ± 4.734, n = 45; overall mean size of all clutches = 4.377 ± 3.624, n = 106.

The relationship between viable clutch size and mean intra-clutch egg volume for each of the three study years is shown in Figure 3.3*a-c*, and the overall relationship is shown in Figure 3.3*d*. None of the individual year graphs show a significant correlation, although when the data are combined egg volume increases significantly with increasing clutch size. In all three years, both clutch size and egg size decreased over the laying season. Figure 3.4 shows the relationship between viable clutch size and ln[date of lay] for each of the three years. Figure 3.5 shows the relationship between mean intra-clutch egg volume (viable clutches only) and laying date for each of the three years (see figure legends for statistical details).

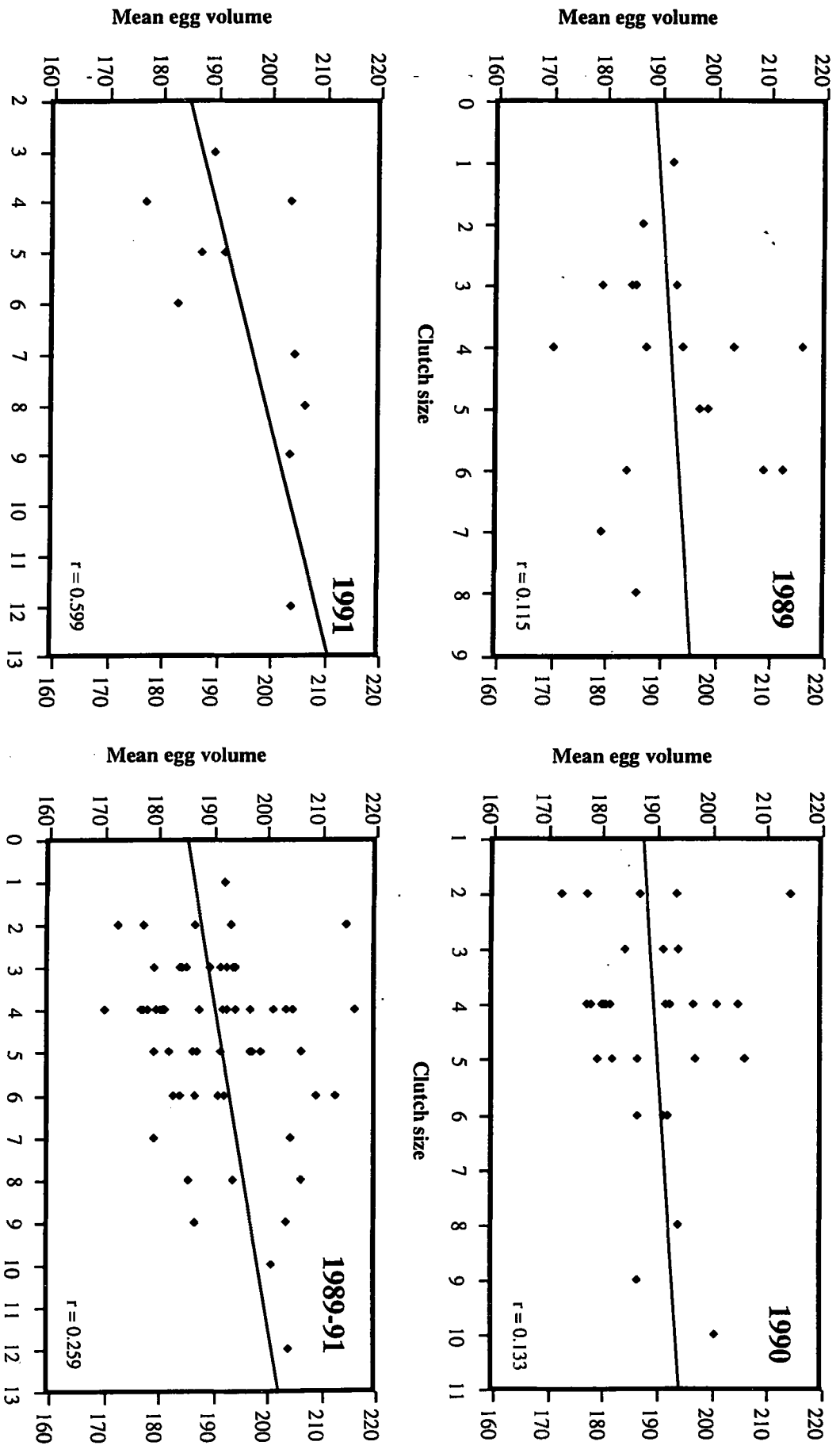


Figure 3.3. Relationship between viable clutch size and mean intra-clutch egg volume. *a-c*: Data from 1989, 1990 and 1991 respectively. *d*: Combined data from all three study years. Data were compared using Pearson's product-moment correlation coefficient: 1989, n = 18, r = 0.1152, n.s.; 1990, n = 31, r = 0.0493, n.s.; 1991, n = 10, r = 0.5990, n.s.; 1989-91, n = 59, r = 0.2589, $p < 0.05$.

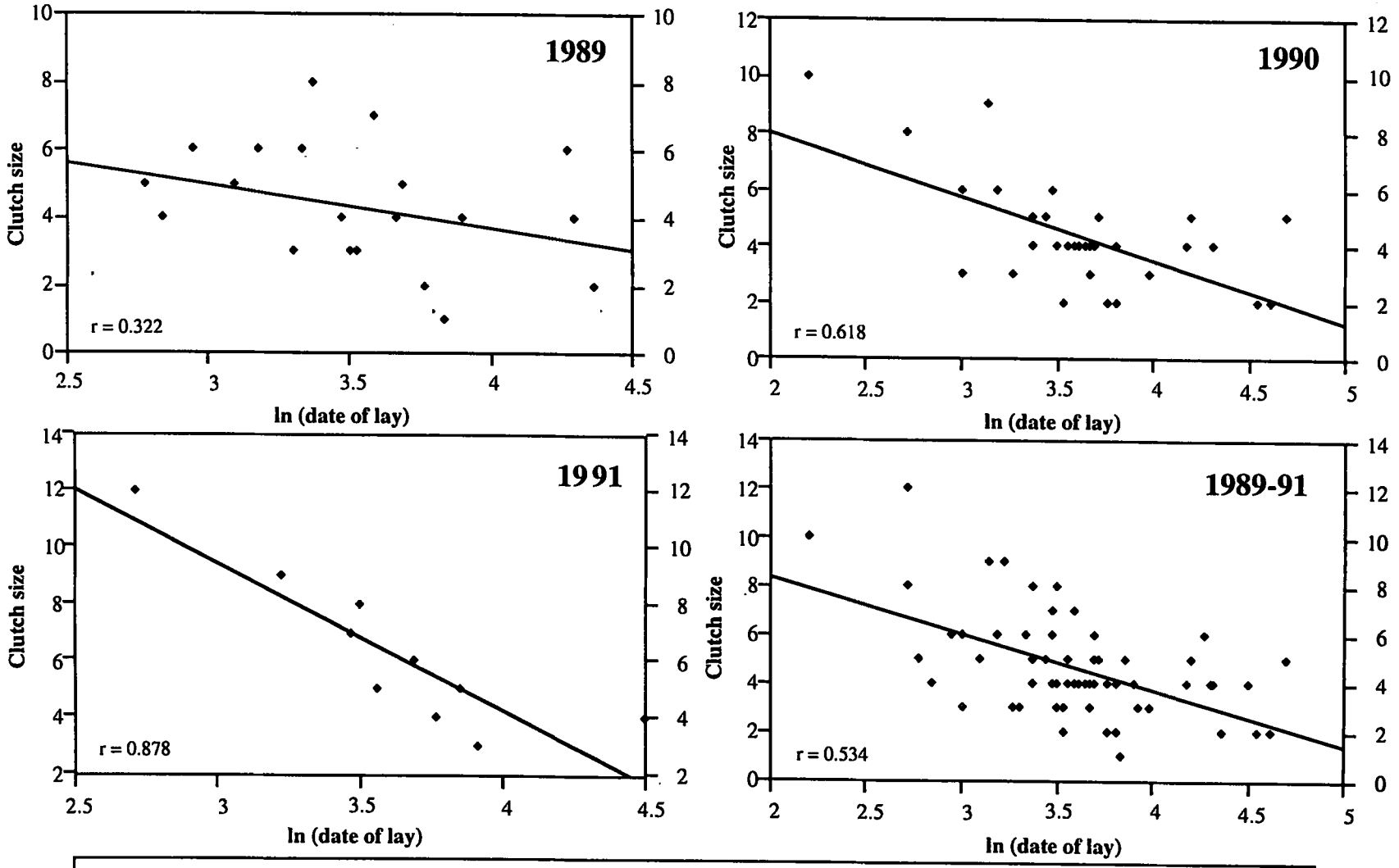


Figure 3.4. Relationship between viable clutch size and mean date of lay (log-transformed). *a-c:*Data from 1989, 1990 and 1991 respectively. *d:* Combined data from all three study years. Pearson's product-moment correlation coefficient: 1989, n = 21, r = – 0.322, n.s.; 1990, n = 31, r = – 0.618, $p < 0.01$; 1991, n = 10, r = – 0.878, $p < 0.05$), and for all years combined (n = 62, r = – 0.534, $p < 0.01$).

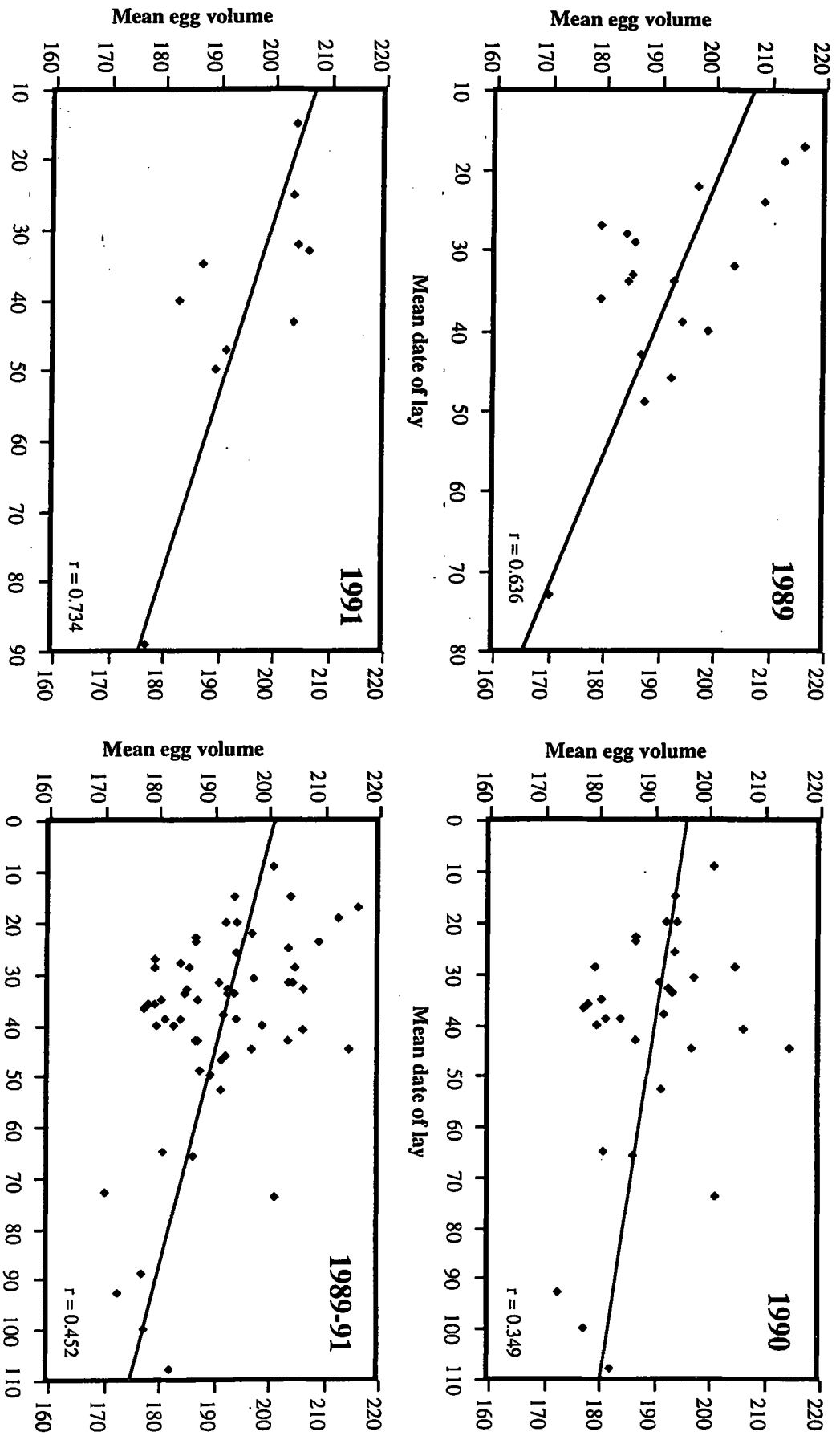


Figure 3.5. Relationship between mean intra-clutch egg volume (viable clutches only) and mean date of lay. *a-c*:Data from 1989, 1990 and 1991 respectively. *d*:Combined data from all three study years. Data were compared using Pearson's product-moment correlation coefficient: 1989, n = 18, $r = -0.6356$, $p < 0.01$; 1990, n = 31, $r = -0.3488$, $p < 0.05$; 1991, n = 10, $r = -0.7344$, $p < 0.05$; 1989-91, n = 59, $r = -0.4522$, $p < 0.01$.

Variation in reproductive expenditure over a breeding season may reflect changes in environmental factors, such as weather or vegetative cover. Figure 3.6 shows mean monthly temperature, rainfall and sunshine for each of the three study years. The majority of peahens made their nests in clumps of nettles, and I assessed nest cover over the season by estimating the average height of nettles over the Park once a week. Plants reached peak height around June/July, and then began to lose their leaves and die back, thus providing less dense cover for any nests. Figure 3.7 shows mean clutch and egg size over the breeding season, in relation to mean estimated nettle height.

Monthly rainfall was much more variable over the three years than either sunshine or temperature (Figure 3.6). Throughout the nesting season (approximately May to August), temperature and sunshine levels are consistently high, and rainfall is at its lowest. This contrasts with the situation in India: the breeding season of native peafowl begins immediately after the start of the monsoon, when rain is torrential but temperatures can be over 40°C (A. Musavi, pers. comm.).

Figure 3.7 shows that the peak of nesting occurs before the peak of nettle growth. This suggests that vegetative cover for the clutches is not the primary determinant of the date of lay, since eggs laid in June are less visible to predators than those laid earlier. Nesting may however be timed so that the peak of hatching coincides with maximum nettle growth, in order to provide cover for newly-hatched chicks. It is also possible that the timing of nesting at Whipsnade is related to India's more tropical seasons: for example, if the growth of nesting vegetation is very consistent throughout the year in India, it may be of less importance than other environmental cues in determining the onset of nesting; however, evidence suggests that drought can have a dramatic effect on nesting vegetation in India (Sharma 1969, 1972; M. Petrie, pers. comm.).

Factors other than nest cover which may promote early nesting include (i) that hens are allowing time for renesting, should the first clutch be unsuccessful; or (ii) that hatching coincides with the peak availability of food for the chicks (Lack 1954, 1968), and the longest growth period before the onset of winter.

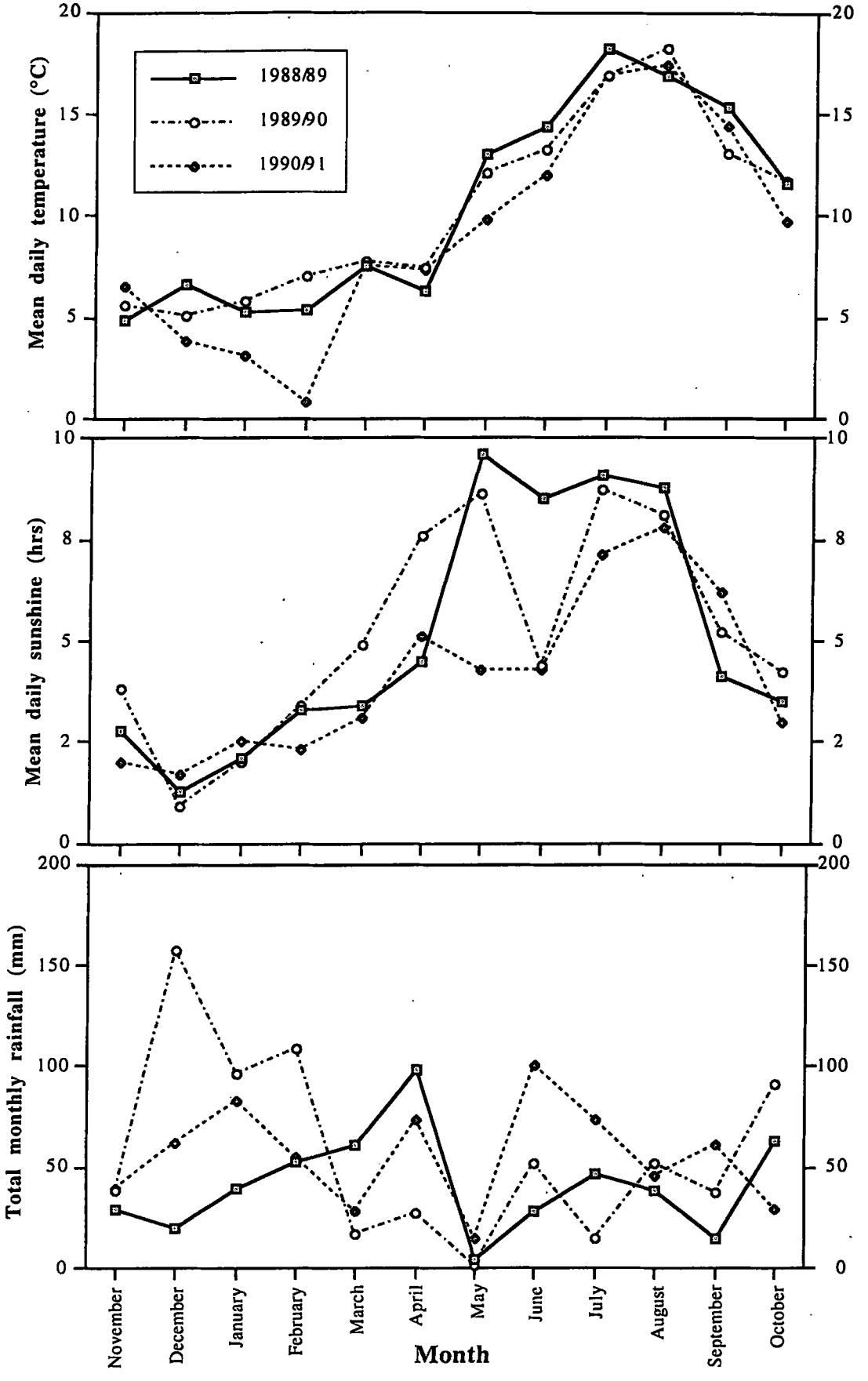


Figure 3.6. Mean monthly temperature (°C), sunshine (hours/day) and rainfall (mm/month) over the three study years (data are from the closest meteorological station at Rothamsted, Hertfordshire; courtesy of The Met. Office, Bracknell, Berkshire).

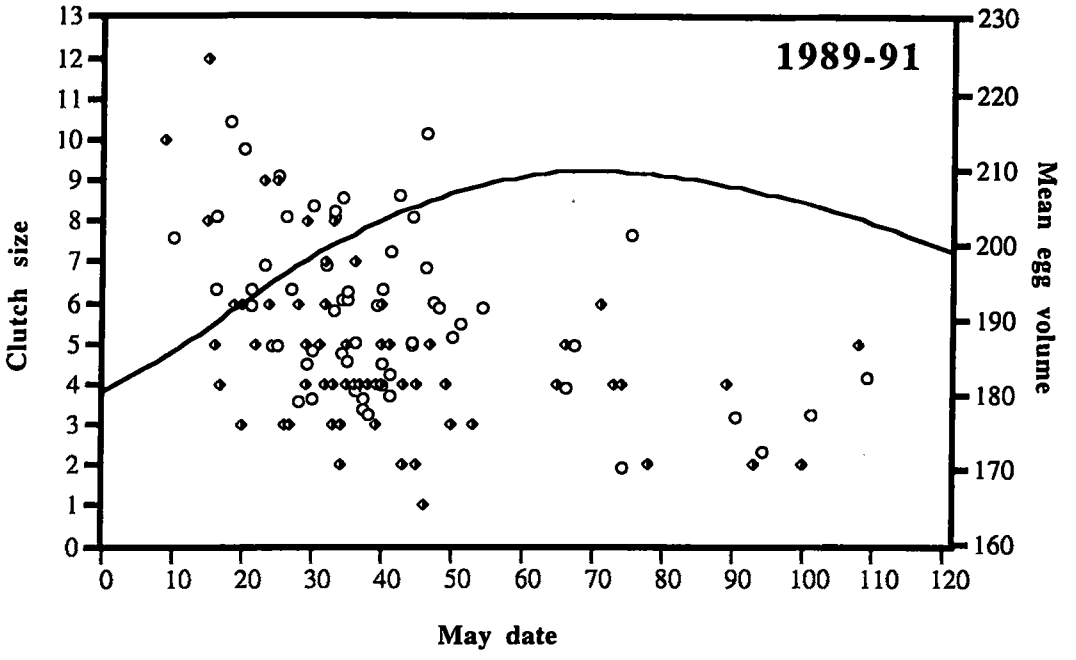


Figure 3.7. Changes in clutch size (diamonds), egg volume (circles), and relative mean nettle height (line) over a season (shown as days after May 1st).

The age of the majority of females is unknown, since once a peahen reaches two years old she has adult plumage and it is not possible to determine her age*. However, some females were caught within their first year, and from subsequent recapture measurements some idea of a growth curve can be obtained. Figure 3.8*a,b* shows how tarsus length and weight change with age; Figure 3.8*c* shows the relationship between weight and tarsus length†. The graphs show not only those hens whose ages were known, but also take account of females which were mature at the time of capture. This was achieved by assigning them a nominal hatching year of four seasons prior to capture; for example, a mature peahen caught over the winter of 1989/90 is known to have hatched in or before 1988, and is thus designated the hatching year 1986.

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* It is possible that spur length may provide a useful indicator of age, but this has yet to be substantiated (M. Petrie, pers. comm.).

† Some of these morphological data have been kindly provided by M. Petrie; the remainder were collected in conjunction with M. Petrie and others (see Section 2.2.2).

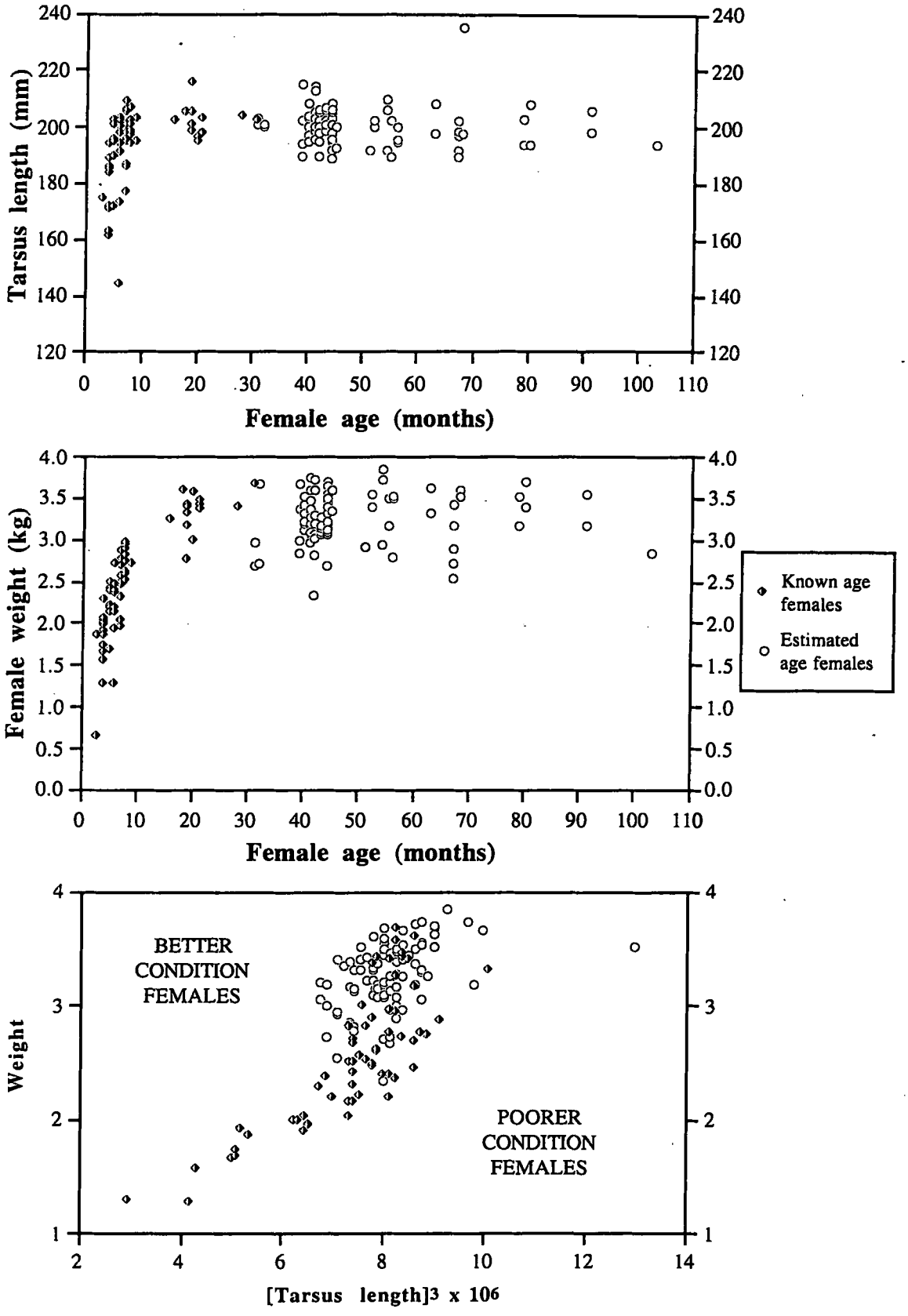

Figure 3.8. *a:* Relationship between female age (in months) and tarsus length (mm). *b:* Relationship between female age (in months) and weight (kg). *c:* Relationship between weight (kg) and tarsus length (mm). In all graphs, known age hens are represented by diamonds, and estimated-age hens by circles.

Since the exact ages of very few marked breeding females were known, few conclusions can be drawn about the relationship between parental age and measures of parental investment, such as clutch size, egg weight or laying date for example. However, the limited information available does allow breeding hens to be divided into two broad age categories: the first group consisting of females known to be aged two, three or four at the time of breeding ($n = 8$), and the other category being females known to be older than four ($n = 23$). Hens whose ages were uncertain but which may have been less than four years old were excluded from the calculations.

Since females cannot be accurately aged once they develop the adult plumage, it cannot be assumed that hens continue to grow larger or heavier once they are past two years of age. Figure 3.8*c* demonstrates that the relationship between tarsus length and weight is very similar for both young and old hens, and it is perfectly possible that young breeding females are heavier than older ones. This can be investigated further by assigning a measure of body condition to each hen.

Using the formula "weight (kg) ÷ [tarsus length (mm)]^3 x 10^5" as an index of body condition, Figure 3.9 shows the relationship between age and condition. It is apparent from Figures 3.8 and 3.9 that weight, tarsus length and condition all increase rapidly with age within the first year, but then reach an asymptote. These morphological measurements cannot therefore be used to ascertain a mature hen's exact age; nevertheless, such measurements are useful in determining the body condition of particular females in relation to one another.

Figure 3.10 shows the mean clutch size, egg volume and laying date for the two age categories of females. There was no significant difference between "young" and "old" females in either clutch size or mean intra-clutch egg volume (Mann-Whitney U test: $p > 0.05$ for both), but "young" hens laid significantly earlier in the season than "old" hens (Mann-Whitney U test: $p < 0.01$).

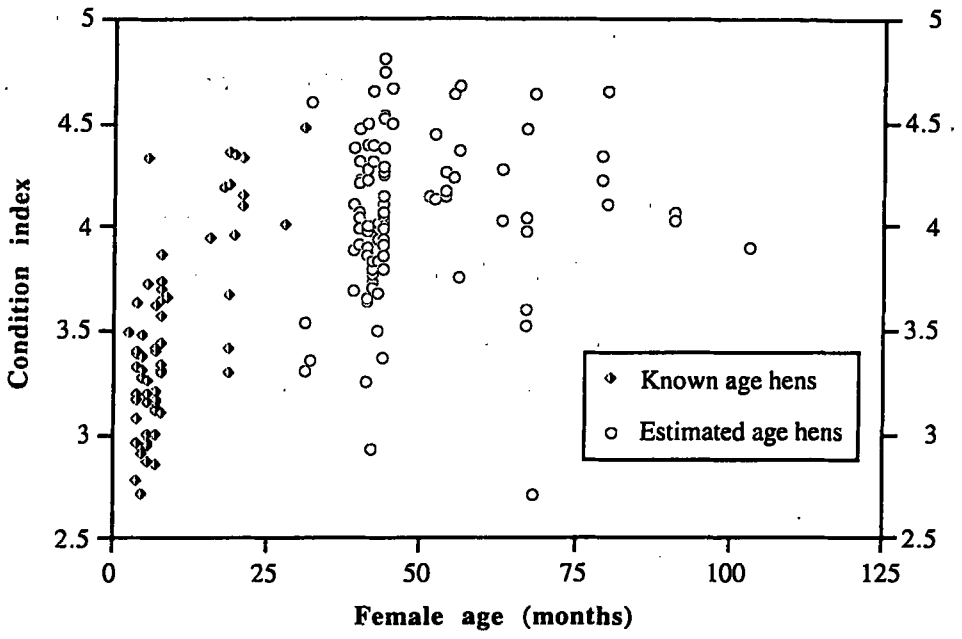

Figure 3.9. Relationship between female age (in months) and an index of body condition ([weight ÷ (tarsus length)^3] x 10^5). As in Figure 3.8, known age hens are represented by diamonds, and estimated-age hens by circles.

Figure 3.11 shows how the body condition of hens changes according to the month of capture. It seems from Figure 3.11*a* that immature females grow fairly steadily throughout the winter, between October and April.

The body weight of mature hens (*i.e.* two or more years old) displays a rather different curve (Figure 3.11*b*): females appear to lose weight over winter, between November and February, but their condition improves rapidly during the spring, between February and April. One might therefore conclude that peahens gain weight more rapidly as the weather becomes warmer and food supplies increase. However, although no mature females were caught and weighed between May and September, Figures 3.11*b* and *c* show that mean body weight in fact decreases during this period (shown by dotted line in Figure 3.11*b*).

Such a decline may simply reflect a drop in the availability of food over the summer, but it would seem to be far more likely that it is a consequence of the expenditure of parental resources on eggs, incubation and caring for chicks. Since the chicks are approaching independence by October (*i.e.* mature enough to feed themselves, keep warm and escape from danger with little assistance from their mother), females may then be released from the

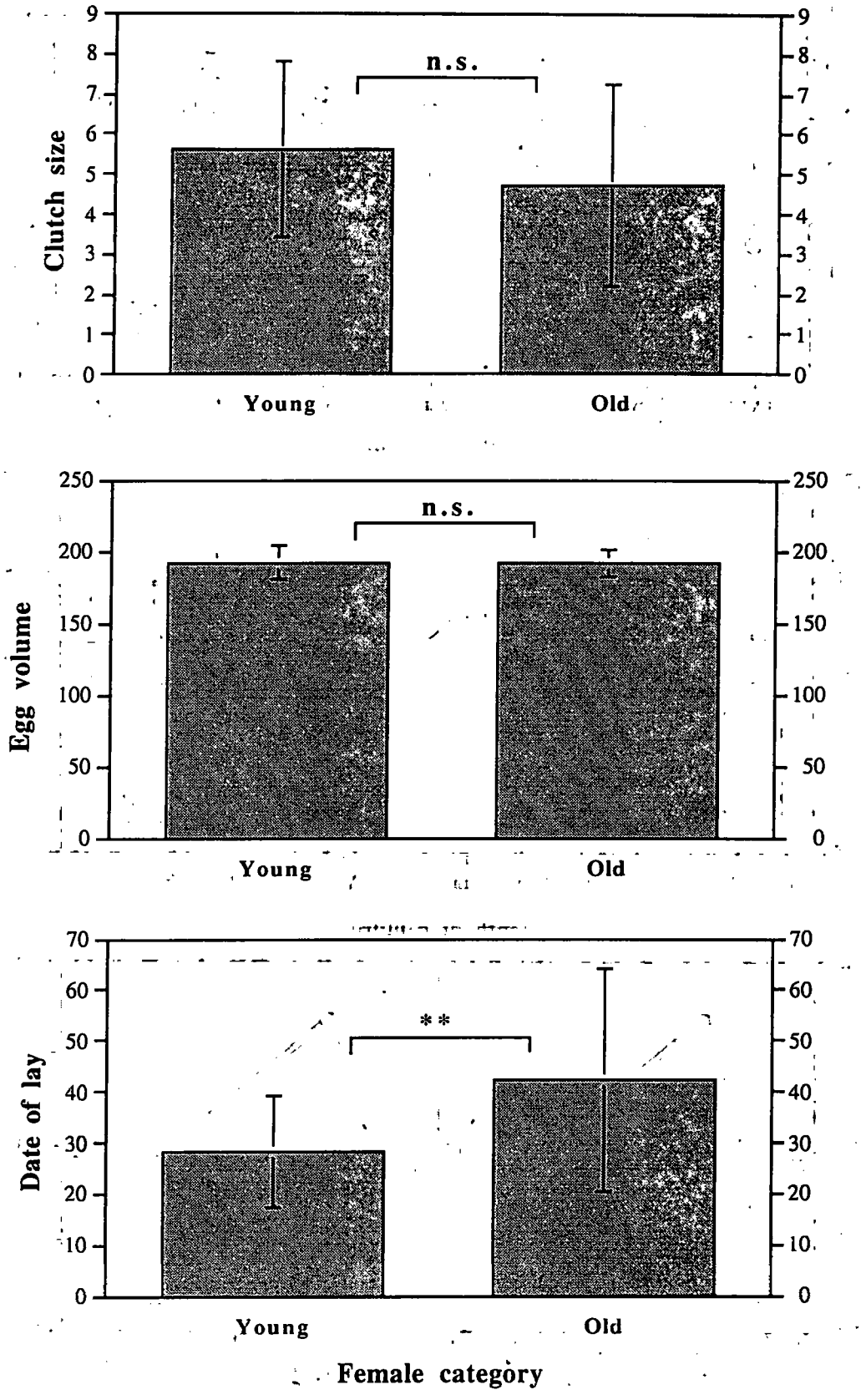

Figure 3.10. Mean clutch size, intra-clutch egg volume and date of lay (May days) of hens in two age categories: (i) "Young" hens known to be aged 2, 3 or 4 at the time of breeding, and (ii) "Old" hens, known to be more than four years old. Error bars represent one standard deviation of the mean. Mean values are compared using a Mann-Whitney U Test: n.s. shows that the difference is non-significant ($p > 0.05$); ** shows $p < 0.01$.

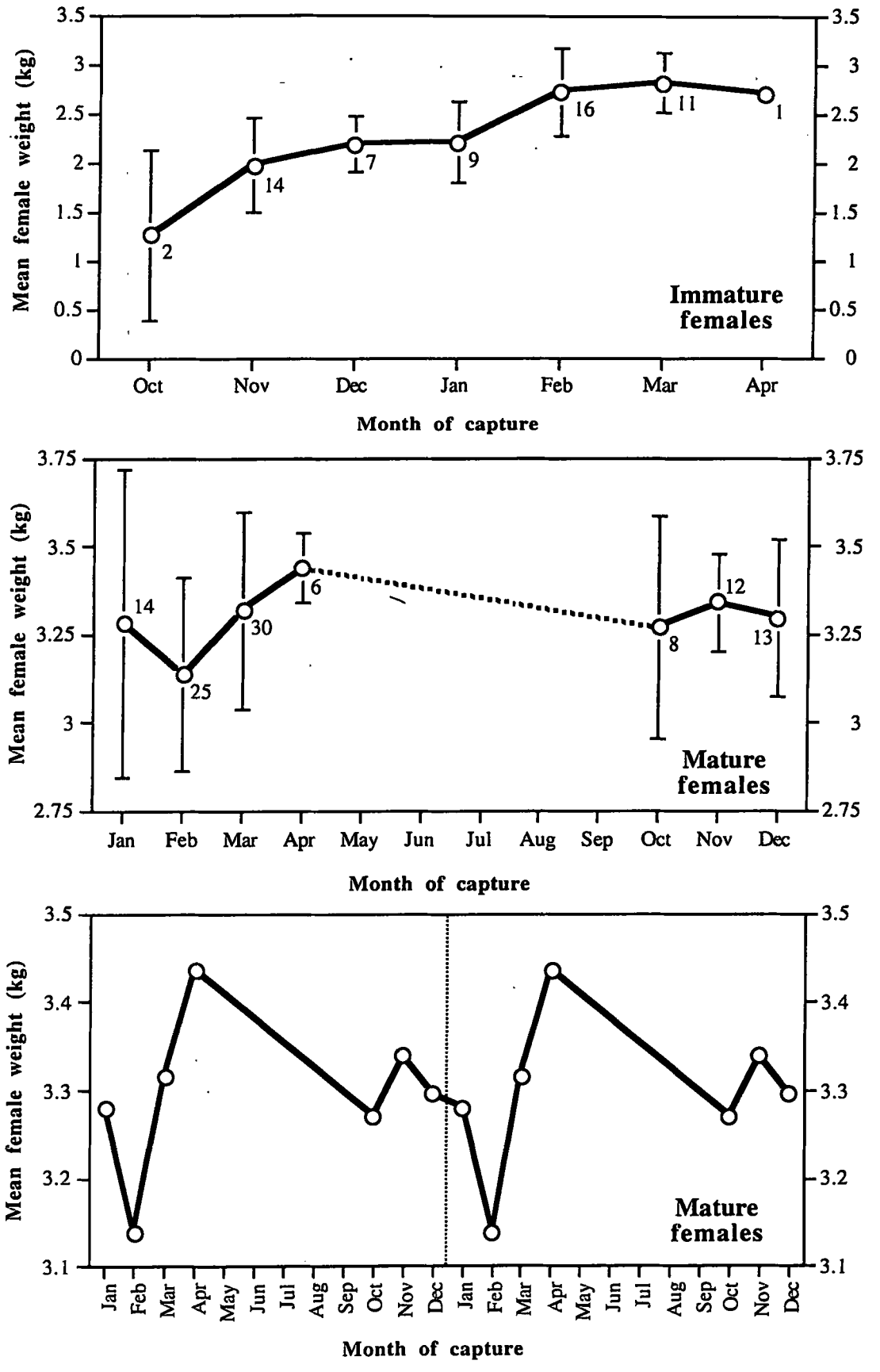

Figure 3.11. Changes in mean female body weight according to the month of capture. *a:* Weight of immature females caught during their first winter. *b:* Weight of mature females (*i.e.* at least two years of age) over a single year. Graphs *a* and *b* show mean weight ± 1 s.d., and the number of hens captured each month. *c:* The data presented in Figure 3.11*b* are repeated over two seasons to illustrate changes in body weight more clearly.

more demanding parental duties, and be able to increase their body condition slightly before the rigours of winter set in. It should be emphasised however that the conclusions drawn here are necessarily tentative, since there are insufficient data to provide firm evidence and the breeding history of hens is unknown at the time of capture.

If we consider only mature hens, variation in body weight is much greater than that of tarsus length (Figure 3.8*c*), even after correcting for the date of capture (Figures 3.11*b* and *c*). These weight differences between females can therefore be used to compare the parental expenditure of hens with relatively higher or lower body condition. As previously explained, it was not possible to obtain morphological measurements of peahens at the time of breeding, and I decided consequently to use the winter weights of females as some indication of their relative weights during the breeding season, taking into account their age, month of capture, and time since the measurements were recorded. When a hen was captured more than once, the mean winter weight was used.

Figure 3.12 shows the relationship between the mean mature winter weight of marked females and *a:* laying date, *b:* clutch size, and *c:* mean intra-clutch egg volume. Although none of the *r* values are significant, the graphs indicate a degree of correlation between the variables. There is a negative relationship between weight and date of lay (*i.e.* heavier hens tend to lay earlier in the season than lighter ones), and female weight is slightly positively related to both clutch size and egg volume.

Although there is a wide range of clutch and egg sizes within the population at Whipsnade, individual females may in fact be consistent between nesting attempts, and the observed variation may thus reflect differences between rather than within hens. In order to determine whether individual females tend to lay the same sized clutches or eggs, I needed to record nesting data from marked hens over two or more breeding attempts. Repeated measures of the clutch sizes and mean intra-clutch egg volume were available from a total of seven hens, and the results are shown in Figure 3.13. The effects of nest parasitism have been removed (see Section 3.4.2). It is apparent both from the graphs and from statistical analysis that females are far more consistent with respect to egg volume (Figure 3.13*b*) than to clutch size (Figure 3.13*a*).

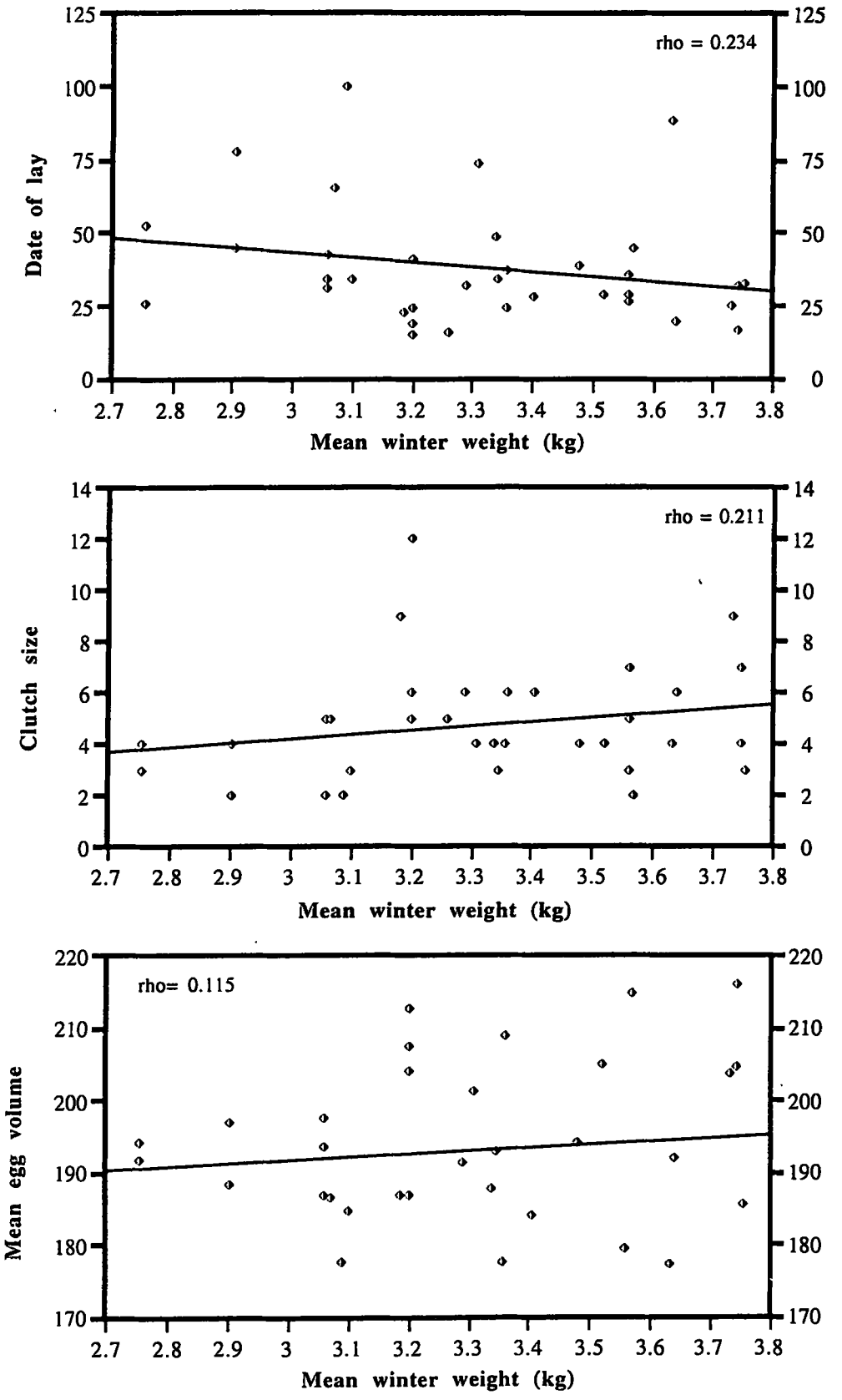

Figure 3.12. Relationship between marked female winter weight and *a:* date of lay; *b:* clutch size; and *c:* mean intra-clutch egg volume (data from all three study years are combined). Data are compared using Pearson's product moment correlation coefficient: *a*, n = 35, r = – 0.234, p > 0.05; *b*, n = 33, r = 0.211, p > 0.05; *c*, n = 32, r = 0.115, p > 0.05.

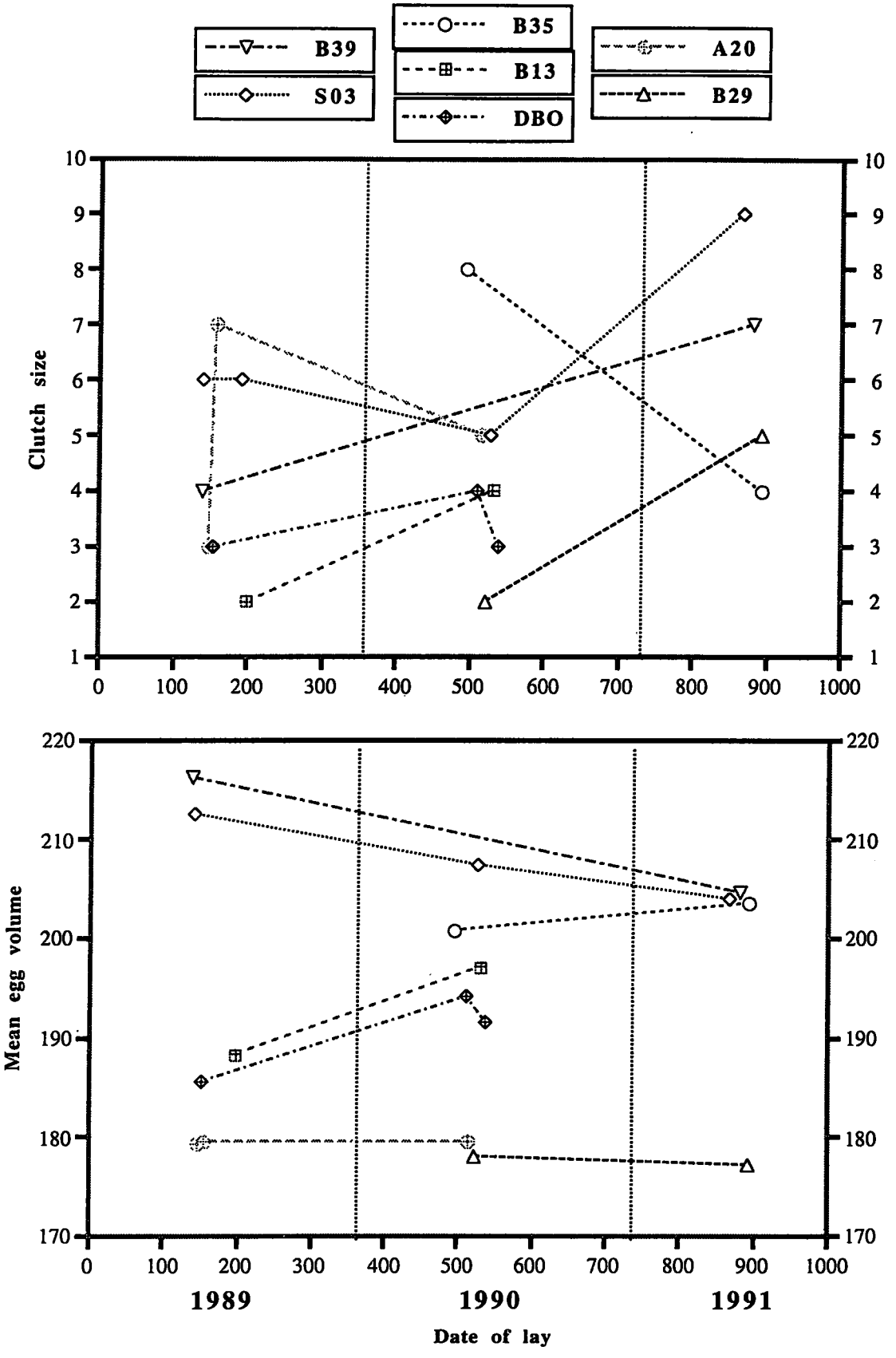

Figure 3.13. Consistency in *a:* clutch sizes and *b:* mean intra-clutch egg volume laid by marked individual females over consecutive years. (The second 1989 egg volume value for female S03 was unavailable.) The horizontal axis represents the date of lay of each clutch as the number of days since January 1st 1989. Consistency was analysed using the Kendall coefficient of concordance: Clutch size, N = 7, k = 3, s = 132, W = 0.5238, $p > 0.05$; Egg size, N = 7, k = 3, s = 252, W = 1.0000, $p < 0.01$).

3.3.2 *Incubation behaviour*

Comparison of the behaviour of incubating females and sitting, non-parent females showed that incubating hens are significantly more likely to display a vigilant posture, remain in attendance at the nest, and of course roll their eggs (Mann Whitney U-test: vigilance, $U = 178$, $p = 0.0294$; nest attendance, $U = 196$, $p = 0.0052$; egg turning, $U = 240$, $p < 0.0001$); consequently I decided to use these particular behaviour patterns as measures of parental expenditure on a clutch.

Figures 3.14-3.17 show the variation in three measures of parental expenditure (vigilance, egg rolling and nest attendance [expressed for ease of comparison as absence from the nest]), in relation to the reproductive value of the clutch; and Figures 3.18 and 3.19 show variation in relation to the residual reproductive value of the female. In Figures 3.14-3.18, graph *a* illustrates relative levels of vigilance; graph *b* shows the proportion of time spent away from the nest; and time allocated to turning eggs is shown in graph *c*. Correlations are analysed using the product-moment coefficient of correlation. As outlined in Section 3.2.2, time budget analysis was used to determine the proportion of time that each female allocated to parental behaviour patterns, and the data are therefore expressed as a percentage of the total observation period.

Clutch reproductive value is measured using four parameters: clutch size, egg volume, stage of incubation, and date of lay. The age and weight of the incubating female are used as an indication of parental residual reproductive value; however, as explained in Section 3.3.1, these variables could not be measured at the time of breeding, and information on female weights was inferred from their weights at the time of capture. Similarly, the ages of very few females were known precisely, particularly for those hens which were accessible for observation on the nest, and consequently the data are pooled into two categories.

Figure 3.14 illustrates parental expenditure on clutches of different sizes. There is a significant correlation between clutch size and level of vigilance, but no significant relationship between clutch size and either absence from the nest or time spent turning eggs.

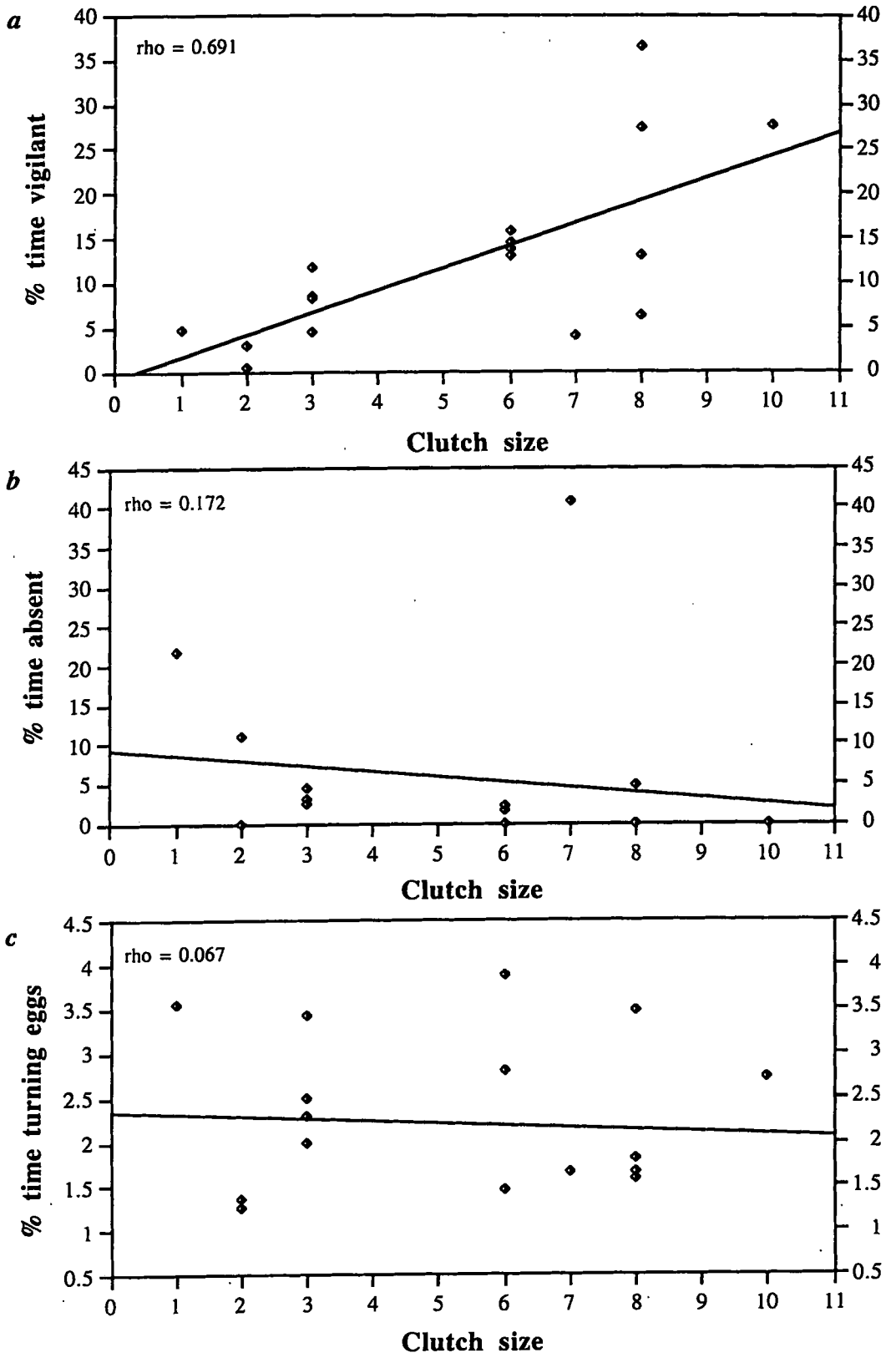

Figure 3.14. Variation in parental expenditure in relation to clutch size. Parental expenditure is expressed in terms of the proportion of the total observation period allocated to *a:* vigilance (n = 17, r = 0.691, p < 0.01); *b:* absence from the nest (n = 17, r = – 0.172, p > 0.05); and *c:* egg turning (n = 17, r = – 0.067, p > 0.05). See text for details.

Figure 3.15 shows variation in expenditure in relation to mean intra-clutch egg volume. Once again, egg volume is significantly related to vigilance, but not to absence or egg-rolling. Parental expenditure on nests at different stages of incubation is shown in Figure 3.16, and there is no significant correlation between incubation stage and any of the measures of parental expenditure. Figure 3.17 illustrates variation in expenditure according to the mean laying date of the clutch, expressed as the number of days since May 1st each year. Yet again, the date of lay is significantly related to the level of vigilance, but there is no correlation with either absence or egg turning.

Parental expenditure in relation to the female's winter weight and age is shown in Figures 3.18 and 3.19 respectively. It appears that there is a significant relationship between female weight and vigilance, but there is no correlation with time absent or egg turning. Since the sample sizes of known female age are rather small, ages have been pooled into two categories in Figure 3.19: "young" (3 or 4 years old, n = 2) and "old" (≥ 6 years old, n = 12). The behaviour patterns of young and old hens were compared using a Mann-Whitney U test: young females were significantly more vigilant than old ones, but there was no significant difference between the two groups either in absence from the nest or in egg rolling behaviour.

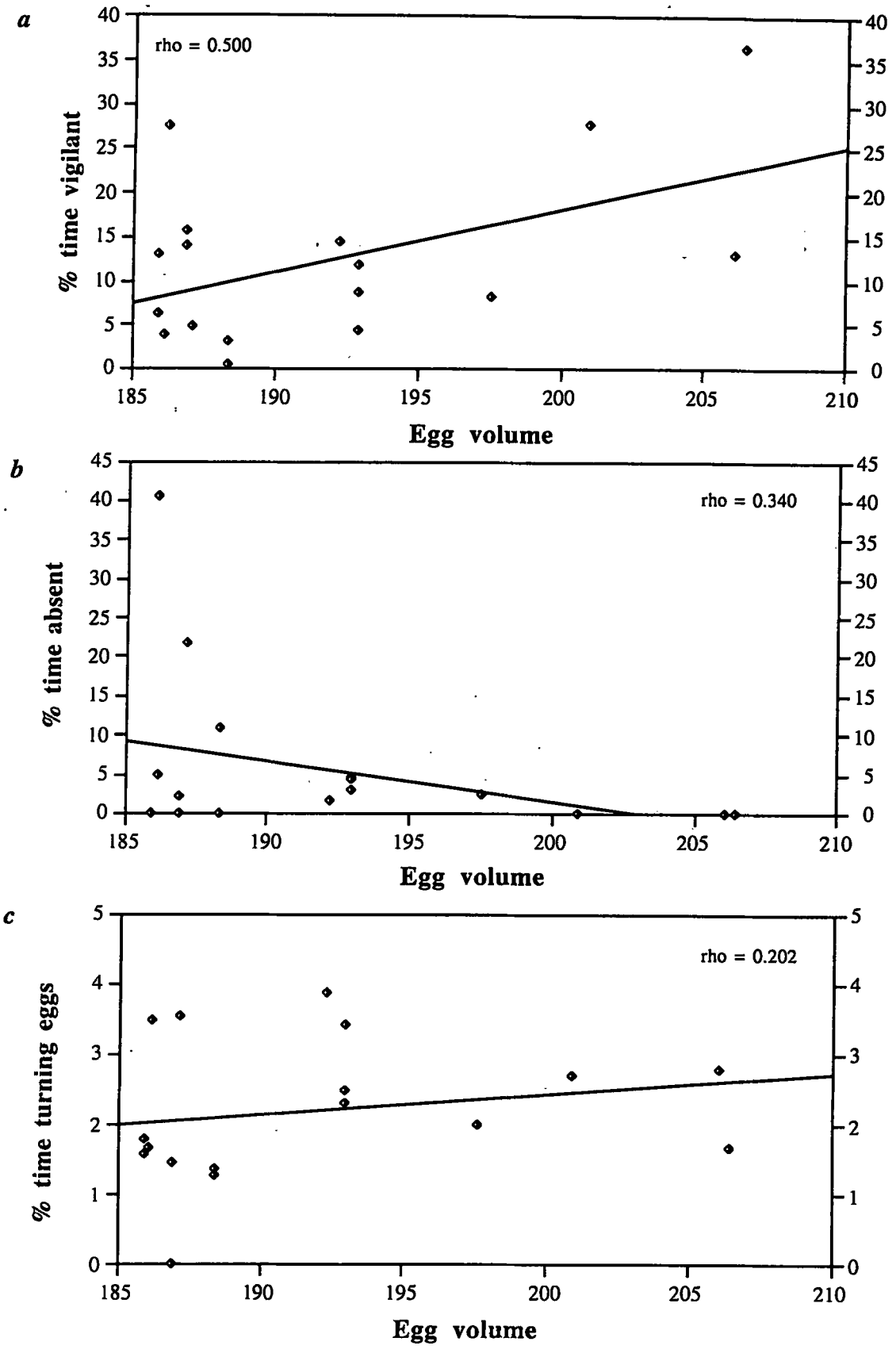

Figure 3.15. Variation in parental expenditure in relation to mean intra-clutch egg volume. Measurements of parental expenditure are as in Figure 3.14. Correlations: *a:* vigilance ($n = 17$, $r = 0.500$, $p < 0.05$); *b:* absence from the nest ($n = 17$, $r = -0.340$, $p > 0.05$); *c:* egg-rolling ($n = 17$, $r = 0.202$, $p > 0.05$).

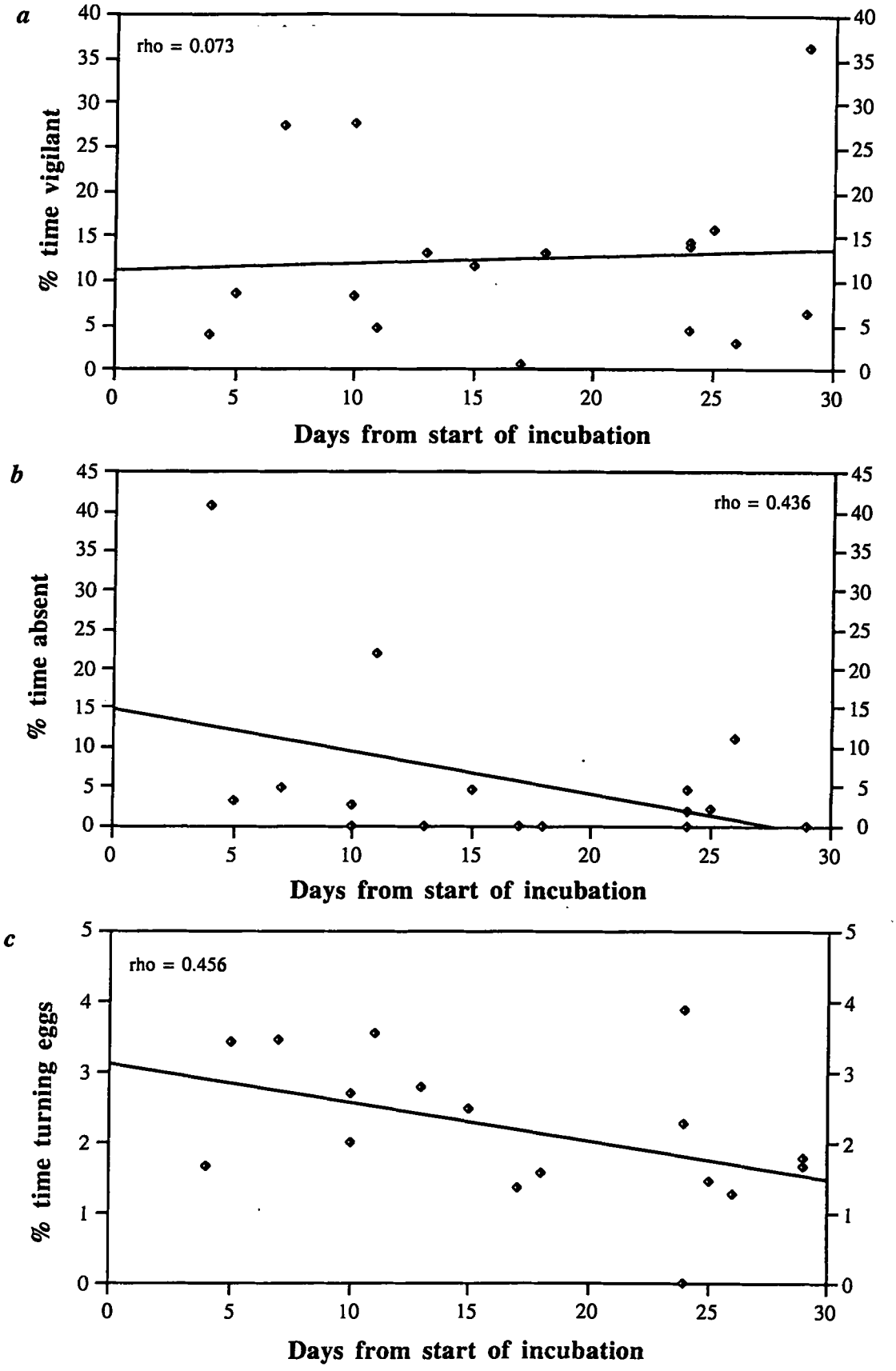

Figure 3.16. Variation in parental expenditure in relation to the stage of incubation. Measurements of parental expenditure are as in Figure 3.14. Correlations: vigilance: n = 17, r = 0.073, p > 0.05; absence: n = 17, r = – 0.436, p > 0.05; egg turning: n = 17, r = – 0.456, p > 0.05.

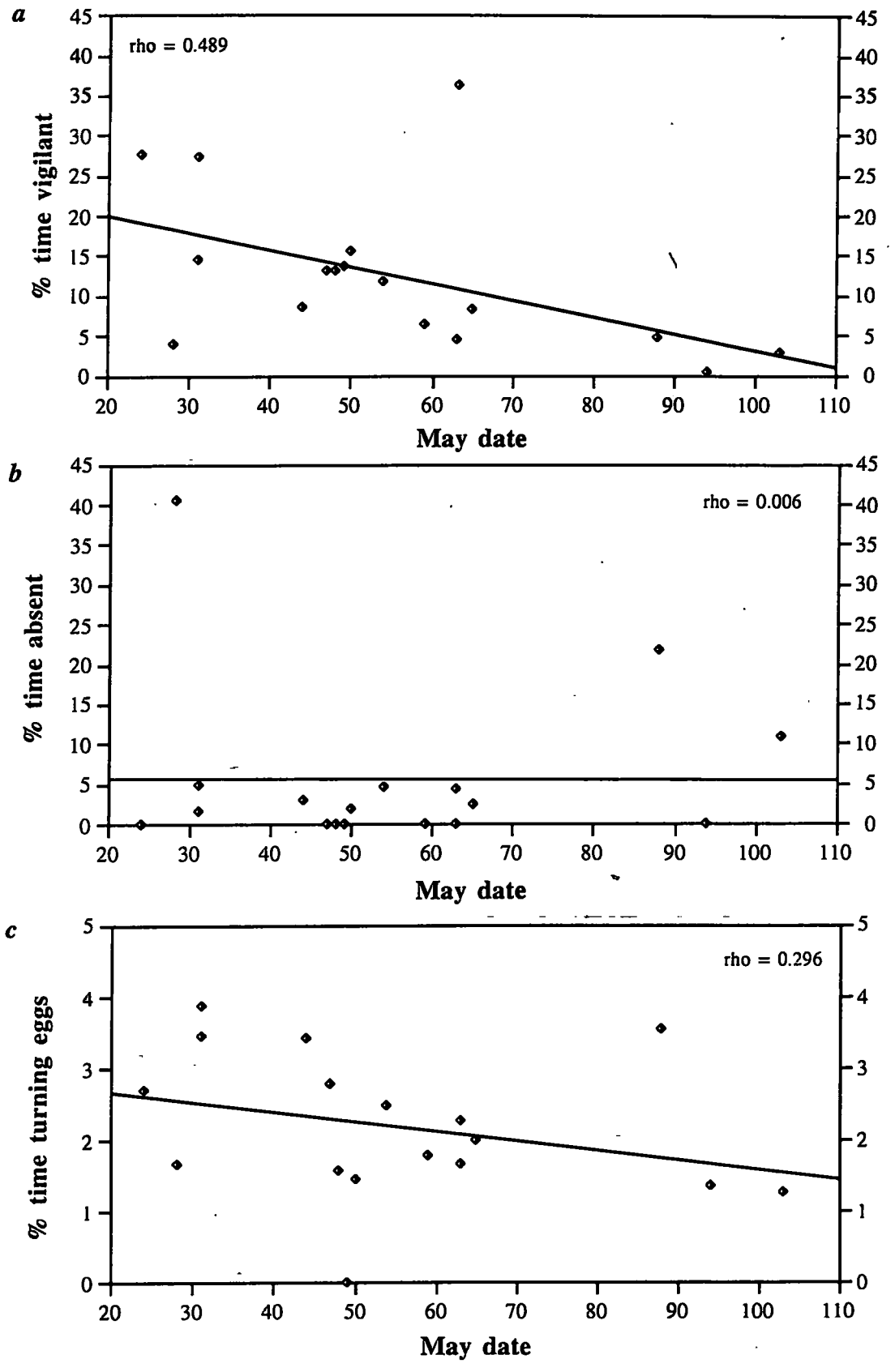

Figure 3.17. Variation in parental expenditure in relation to the laying date of the clutch, expressed as the number of days since May 1st in the year of breeding. Measurements of parental expenditure are as in Figure 3.14. Correlations: vigilance, n = 17, r = – 0.489, $p < 0.05$; absence, n = 17, r = – 0.006, $p > 0.05$; egg turning, n = 17, r = – 0.296, $p > 0.05$.

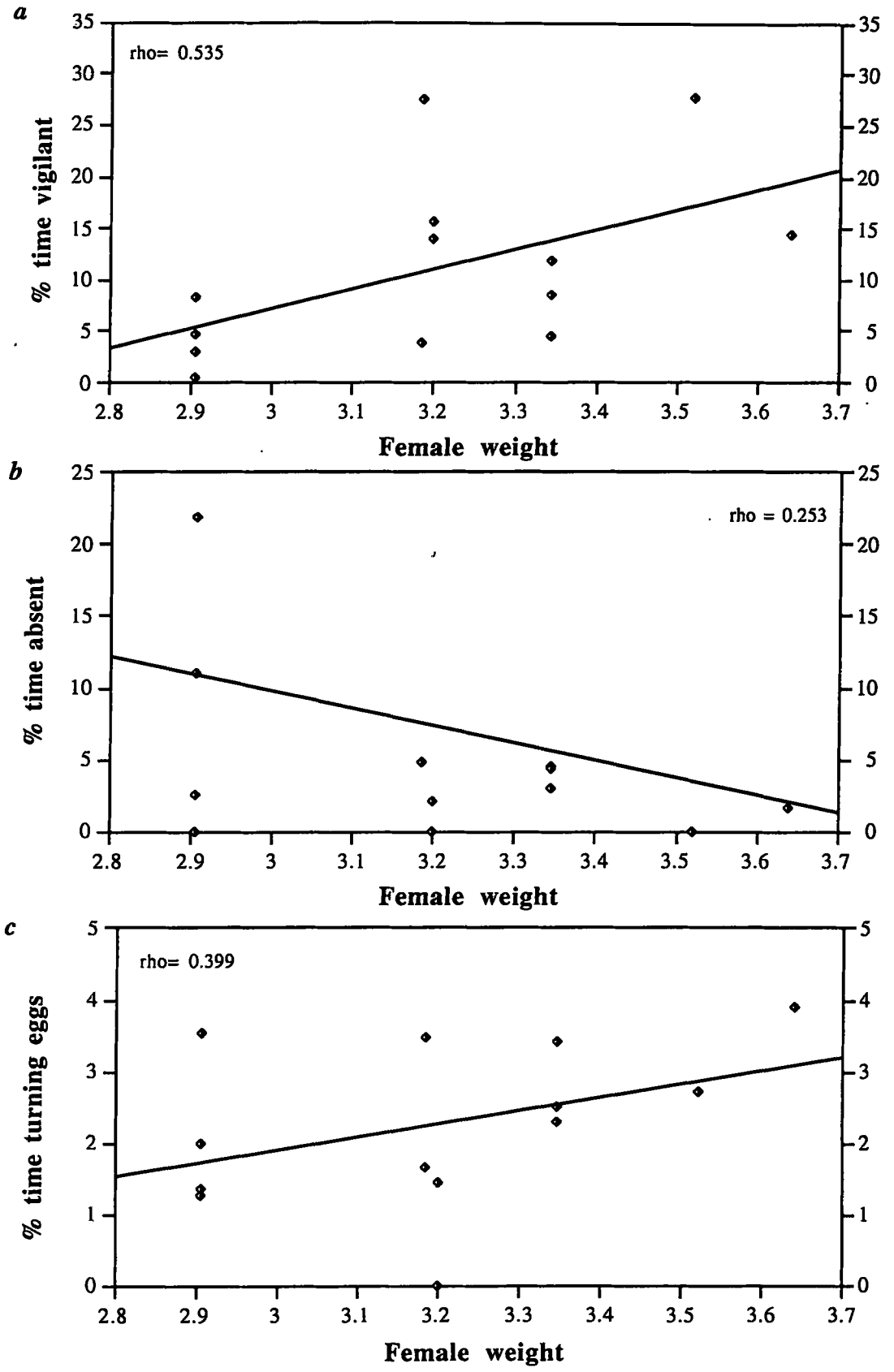

Figure 3.18. Variation in parental expenditure in relation to female winter weight, taken at the time of capture. Measurements of parental expenditure are as in Figure 3.14. Correlations: vigilance, n = 13, r = 0.535, $p < 0.05$; time absent, n = 13, r = – 0.253, $p > 0.05$; egg turning, n = 13, r = 0.399, $p > 0.05$.

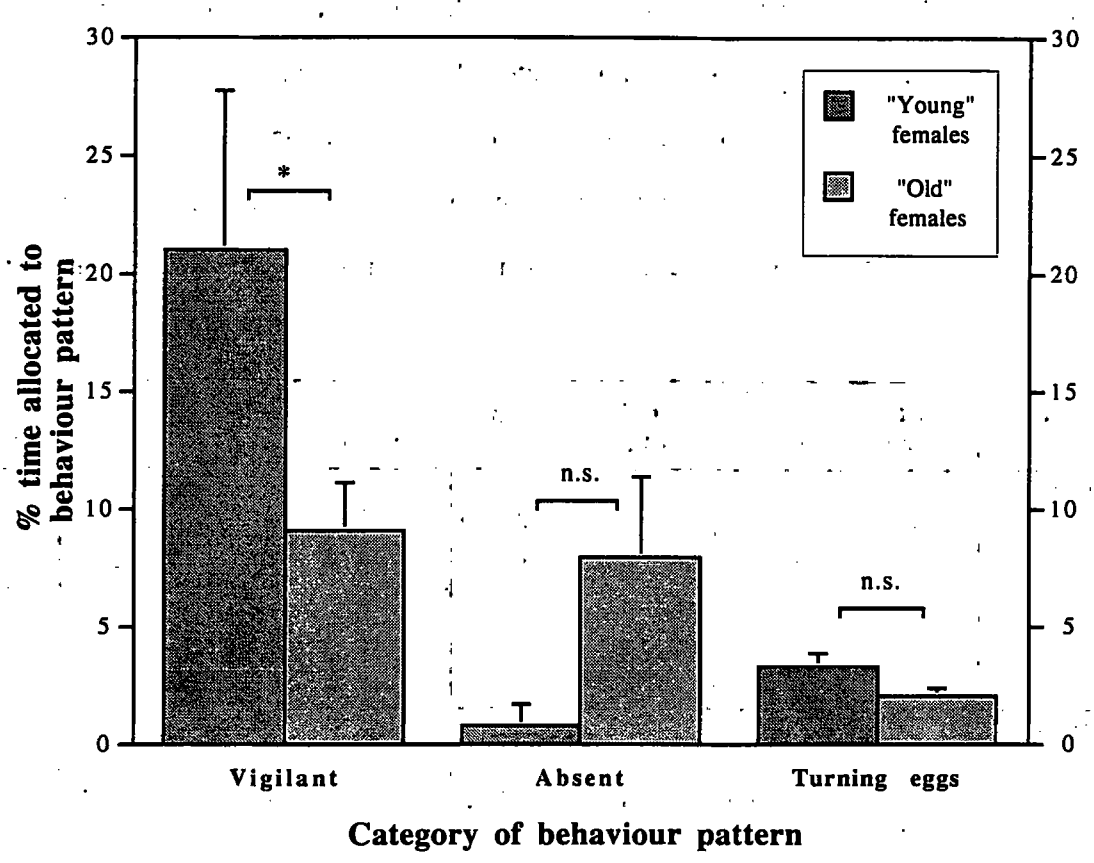

Figure 3.19. Variation in parental expenditure in relation to female age, categorised as either "young" (≤ 4 years old) or "old" (≥ 6 years old). Measurements of parental expenditure are as in Figure 3.14; bars indicate standard errors. Data are compared using Mann Whitney U test; vigilance: U = 2, p = 0.05; absence: U = 19.5, p > 0.05; egg rolling: U = 3, p > 0.05.

The Figures above demonstrate that not all of the measures of parental expenditure used are related to the reproductive value of either the clutch or the female. In particular, the degree of attendance at the nest is not correlated with any of the reproductive value variables recorded, although there is a tendency for nest attendance to increase with increasing clutch size. Similarly, the relationship between vigilance and female age is in the direction opposite to that predicted by reproductive value theory: young hens are significantly more vigilant than old hens. Vigilance levels however are significantly positively correlated with parental weight, and with three of the four measures of clutch reproductive value (*i.e.* clutch size, egg volume, and laying date). The proportion of time spent turning eggs is not significantly correlated with any of the factors measured, although the relationship with incubation stage is nearly significant at the 5% level. However, the direction of the relationship is not as expected from reproductive value theory, which predicts that females should increase their investment over the course of incubation.

Although Figures 3.14-3.19 reveal the nature of the *individual* relationships between parental behaviour and measures of parental and offspring reproductive value, it is known from the results outlined in Section 3.3.1 that some of these variables are not independent. The behaviour patterns observed may be influenced by factors acting in association with each other, and it is therefore desirable to perform multivariate analysis on the data (Table 3.3).

Measure	Clutch size	Egg volume	Incub. stage	May date	Female weight	Female age	Inter-cept	Signif-icance
Vigilance								
(i) all factors	3.025	0.303	– 0.052	0.086	7.261	2.737	– 92.943	
p =	*0.1502*	*0.5964*	*0.8952*	*0.7924*	*0.7771*	*0.7949*	*0.5542*	*0.1727*
(ii) signif. factors	2.612						– 0.947	
p =	*0.0005*						*0.7547*	***0.0007***
Absence								
(i) all factors	– 1.224	– 1.480	– 0.679	– 0.114	– 11.377	– 9.863	366.748	
p =	*0.7338*	*0.1631*	*0.3442*	*0.8453*	*0.8038*	*0.6017*	*0.2038*	*0.6023*
(ii) signif. factors		– 1.244	– 0.693				255.378	
p =		*0.0627*	*0.0676*				*0.0490*	***0.0686***
Turning								
(i) all factors	– 0.296	– 0.072	– 0.093	– 0.001	2.302	– 1.980	15.117	
p =	*0.3010*	*0.3737*	*0.1103*	*0.9809*	*0.5223*	*0.1926*	*0.4910*	*0.2435*
(ii) signif. factors	– 0.186		– 0.077			– 2.088	8.185	
p =	*0.1542*		*0.0420*			*0.0342*	*0.0030*	***0.0892***

Table 3.3. Multiple regression analysis of parental behaviour patterns in relation to measures of offspring and female reproductive value. Multiple regression equations are calculated for each of the patterns analysed (vigilance, absence from the nest, and time allocated to turning eggs), and two sets of coefficients are given: (i) taking into account all of the reproductive value variables measured; and (ii) after stepwise regression, using only those variables which give rise to the most significant overall relationship. P values are given for each of the coefficients, and for the whole regression equation.

Multiple linear regression model	Significance	Equation
$v = 2.6119cs - 0.9472$	p = 0.0007	*Equation 3.4a*
$a = -1.2437ev - 0.6928is + 255.3776$	p = 0.0686	*Equation 3.4b*
$t = -0.1860cs - 0.0770is - 2.0879fa + 8.1851$	p = 0.0892	*Equation 3.4c*

Table 3.4. Multiple regression models which best predict the levels of parental behaviour displayed. P values represent the overall significance of the regression fit of each equation. Notation: v = vigilance, a = absence from the nest; t = time spent turning eggs; cs = clutch size; ev = mean intra-clutch egg volume; is = incubation stage; and fa = female age.

The models described in Table 3.4 demonstrate which of the factors measured are most important in determining the level of parental expenditure. Vigilance is related significantly only to clutch size; absence from the nest is best determined by egg volume and stage of incubation; and time spent turning eggs appears to be most influenced by three factors, clutch size, incubation stage and female age. It should be pointed out that only the equation for vigilance is significant at the 5% level, although the other two equations would be significant at the 10% level. Both vigilance and nest attendance change in the direction predicted by reproductive value theory (*i.e.* they increase as clutch reproductive value increases); however, the level of egg turning is negatively related to measures of both clutch reproductive value and parental residual reproductive value. The results of these analyses will be discussed further in Section 3.6.

3.4 Nest parasitism and dump-nesting (pre-hatch brood amalgamation)

3.4.1 Egg dumping at Whipsnade

In Chapter One I distinguished between the similar phenomena of egg dumping and intraspecific nest parasitism. Egg dumping is defined as the abandonment of eggs, often in exposed positions with no obvious nest scrape; the eggs are not incubated, and females are never observed in the vicinity of a dump nest. In contrast, nest parasitism involves the deposition of an egg into a nest incubated by another female, and this will be discussed in Section 3.4.2.

Two modes of egg dumping have been observed at Whipsnade, and typical examples are shown in Plates 3.2-3.4. One category consists of single abandoned eggs, which were almost exclusively found lying on the ground with no protective vegetation (Plate 3.2) - almost as though the peahen had merely dropped the egg as she walked along! In 1989, seven of these single eggs were discovered, 14 in 1990, and six in 1991, giving a total of 27 over the three years of observation.

Plate 3.2. Non-viable clutch seen at Whipsnade: single abandoned egg.

Plate 3.3. Non-viable clutch seen at Whipsnade: large dump nest, laid by several females.

Plate 3.4. Non-viable clutch seen at Whipsnade: large dump nest, laid by several females, in corner of animal shed.

The second category again consists of abandoned, unincubated eggs, but in this case the eggs were clumped together into huge clutches of up to 20 eggs. Most of the dump nests seen were in fairly exposed situations, but unlike the single eggs, many of these clutches appeared to have been laid in locations with some kind of landmark, such as next to a fence, at the foot of a tree, or in the corner of a disused animal shed (*e.g.* Plate 3.4). Large dump nests were not as common as single abandoned eggs: only one was found in 1989, three in 1990, and five in 1991, giving a total of nine over the three years. Mean clutch size is 11.89 $\pm$ 4.70. It can be seen from Figure 3.13 that individual hens are very consistent with respect to the sizes of eggs they lay, and variation in individual egg volume is significantly greater within dump nests than within viable nests (Figure 3.20), suggesting that the eggs are laid by several females.

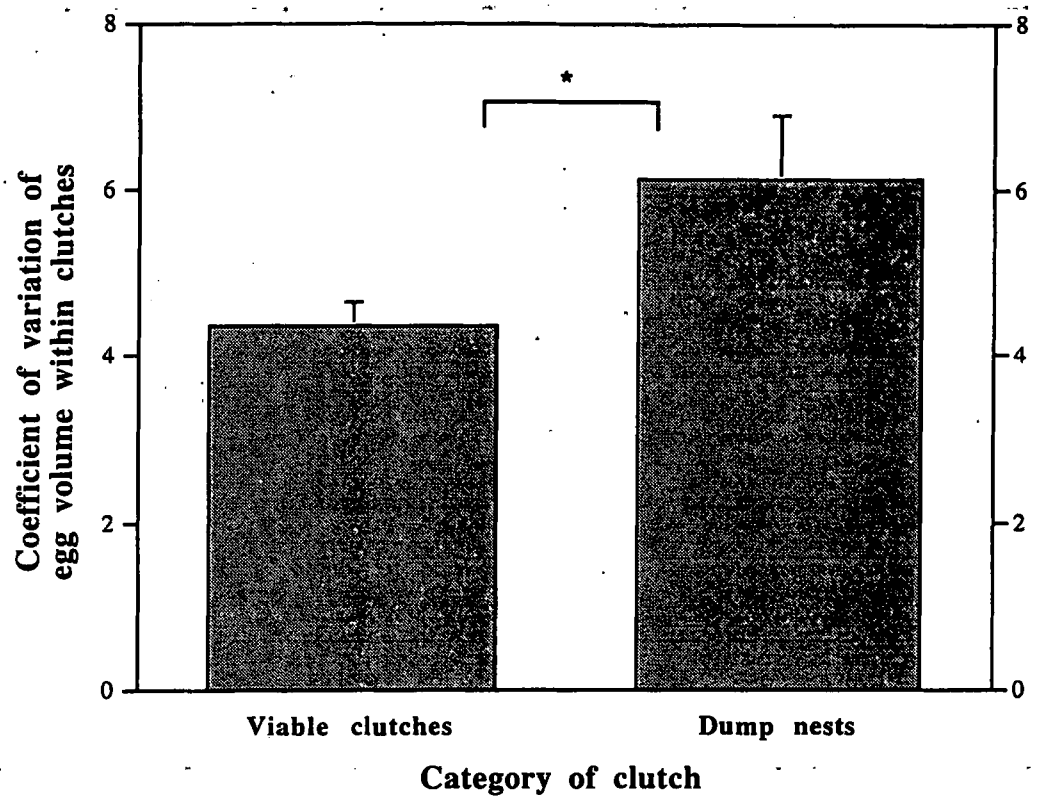

Figure 3.20. Intra-clutch variation in individual egg volume for viable clutches and dump nests. The vertical axis represents the coefficient of variation of egg volume within clutches (= 100 x standard deviation ÷ mean); bars represent the standard error of this value. Data were compared using a t-Test (n_1 = 58 clutches; n_2 = 11 clutches; one tailed test; p = 0.0143).

The mean date of lay of viable clutches is June 9th (± 2.666 days), that of single eggs is May 28th (± 2.779 days), and that of dump nests is May 20th (± 3.074 days). Both single abandoned eggs and large dump nests are laid significantly earlier in the season than viable clutches (two tailed t-Tests: p = 0.0018 and p = 0.00001 respectively), and dump nests occur significantly earlier than single eggs (p = 0.0298) (Figure 3.21).

The mean egg volume of viable clutches is 191.479cm^3 (± 1.397), that of single eggs is 200.444cm^3 (± 3.089), and that of dump nests is 198.927cm^3 (± 2.180). The mean egg volume of both single eggs and dump nests is significantly greater than that of viable clutches (one tailed t-Tests: p = 0.0064 and p = 0.0075 respectively), but there is no significant difference in mean egg volume between single eggs and dump nests (p = 0.3454) (Figure 3.22).

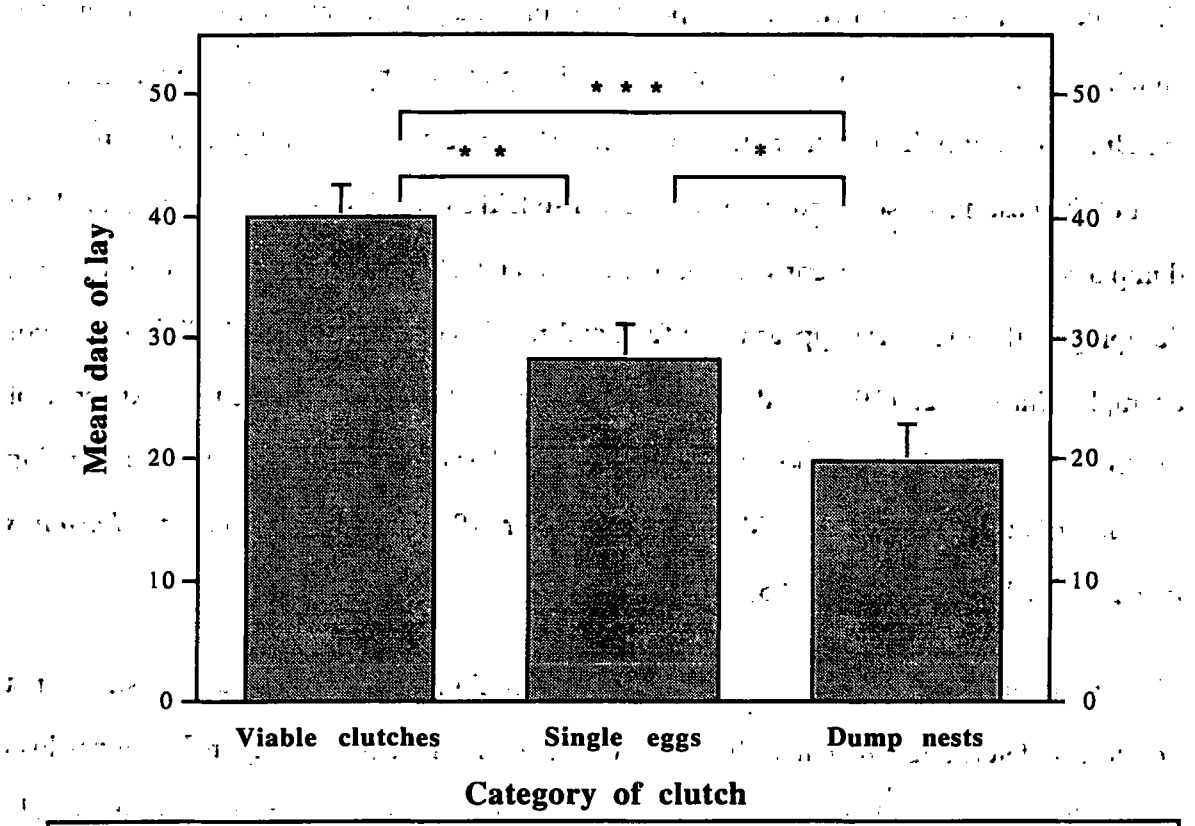

Figure 3.21. Mean laying date (in May days) of viable clutches, single abandoned eggs, and larger dump nests. Bars represent one standard error of the mean. Data were compared using t-Tests (viable nests, n = 62; single eggs, n = 23; dump nests, n = 16), and asterisks denote significant differences between the categories: * indicates $p < 0.05$; ** = $p < 0.01$; and *** = $p < 0.001$.

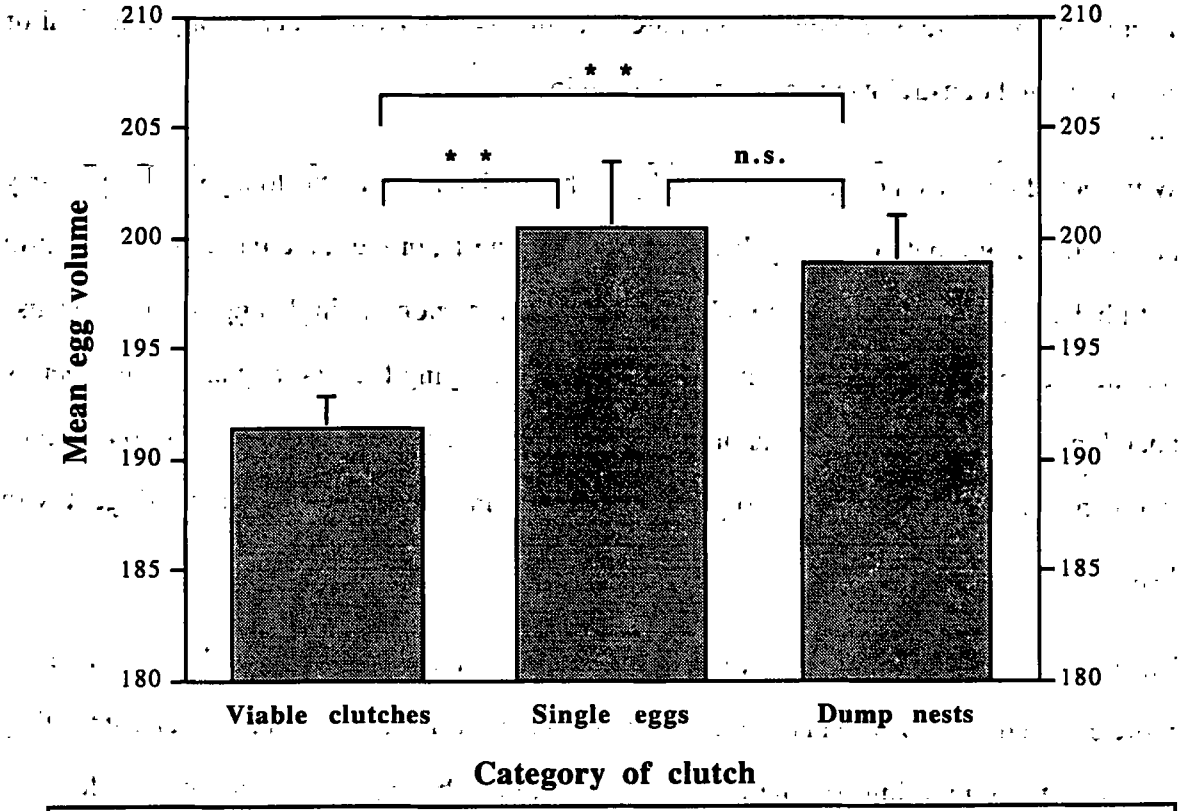

Figure 3.22. Mean intra-clutch egg volume of viable clutches, single abandoned eggs, and larger dump nests. Bars represent one standard error of the mean. Data were compared using t-Tests (viable nests, n = 59; single eggs, n = 23; larger dumped clutches, n = 15), and asterisks denote significant differences between the categories: n.s. indicates $p > 0.05$; and ** indicates $p < 0.01$.

The types of nests described above appear to be markedly different from viable, incubated clutches in several ways. They are not incubated or protected by vegetation, and dump nests are almost certainly laid by more than one hen. Dump nests are generally found at the very start of the nesting season, and single eggs are also laid earlier than viable clutches; and both dump nests and single eggs consist of larger eggs than viable clutches. Accounts of true egg dumping in the literature appear to be few, and restricted mainly to the Galliformes. For example, Christensen (1954) and Mackie & Buechner (1963) both reported the existence of random or "dropped" eggs prior to nesting in the chukar *Alectoris graeca*; collective laying was described in the chukar by Mackie & Buechner (1963) and in the pheasant *Phasianus colchicus* by Wagner *et al.* (1965).

Since no female was ever observed in the vicinity of either type of non-viable nest, it is not possible to determine which hens have laid there, and I can therefore only make suggestions about why females might adopt such a strategy. At first sight the behaviour seems extremely maladaptive, since eggs deposited either in dump nests or as single eggs will not be incubated and consequently are certain not to hatch, and thus represent wasted expenditure. There may be reasons however which are not adaptive, but which act as physiological or environmental constraints to the females' behaviour.

Why should females indulge in this activity? The motivation for hens to lay single eggs may be different from that governing deposition in dump nests; or the same factor(s) may control both behaviour patterns. It is possible that the phenomenon of single eggs occurs because females begin to make a nest, but are disturbed after laying the first egg and consequently abandon the clutch. This explanation however appears unlikely, since there is no evidence that hens are making any effort to protect the clutch in a nest scrape, or camouflage it with vegetation.

The single eggs observed may have been stolen from viable clutches by predators, and left in more exposed locations. This activity could not be performed by avian predators, since they attack eggs by piercing the shell, and they would not be capable of moving whole eggs. Mammalian predators such as stoats or weasels are probably able to roll complete eggs away from nests, but there was no indication (such as scratches or tooth marks) that the eggs had

been attacked in any way. There were also very few nests found in the vicinity of single eggs (*i.e.* within a radius of 30 metres), and there was no evidence that those nearby nests suffered any losses. In addition, upon discovery of a single abandoned egg I took the usual measurements and photograph, and then returned the egg to its original position; subsequent monitoring of each egg (exact location, stains on the shell, *etc.*) indicated that none had been moved at all since marking.

The possible reasons suggested above for the occurrence of abandoned single eggs are even less likely explanations for dump nests. Such clutches are almost certainly laid by several hens, and so cannot result from the disturbance of a laying female after starting a nest; similarly, dump nests are rarely protected in any way by vegetative cover. Mammalian predators would be unlikely to roll stolen eggs into such huge collections and leave them undamaged, and two of the dump nests were discovered in locations into which it would be impossible to roll eggs.

One potentially adaptive explanation of why females might "dump" their eggs in a communal clutch, with no intention of incubating it, is related to the strategy of intra-specific nest parasitism (see following Section). Hens may be attempting to parasitise the nest of a conspecific (*i.e.* depositing an egg in what appears to be another hen's nest, to save themselves the costs of incubation), while unaware that the clutch is in fact unattended and will not be incubated. However, this theory does not explain the occurrence of single abandoned eggs, or the unprotected location of dump nests; nor does it account for the fact that both single and dumped eggs are larger than those of viable clutches (unless parasitic females are attempting to gain a competitive advantage for their chicks within the subsequent brood, but the level of intra-brood competition is generally low in precocial species such as peafowl).

The phenomena observed may therefore be the outcome of physiological or environmental constraints acting on peahens early in the season. To understand which factors may be influential in this way, it is necessary to review the physiological basis of egg-laying behaviour in birds.

Female birds possess a single ovary, which enlarges in the breeding season, and ova develop sequentially from follicles in the ovarian cortex (Mackie & Buechner 1963; Welty & Baptista 1988). The pattern of growth and maturation of ovarian follicles is regulated by follicle stimulating hormone (FSH) from the anterior pituitary gland. Luteinising hormone (LH) from the same gland induces the release of the ovum from the follicle, and at a later stage the pituitary gland will release prolactin, which depresses FSH and LH and initiates "broodiness" (*i.e.* nesting and incubation behaviour) (Eisner 1960).

Following insemination, sperm is stored in tubules in the utero-vaginal junction with the infandibulum, for a period of between a few hours and two months, depending on the species. At ovulation the ovum is released from the follicle and passes through the oviduct under the influence of the ovarian hormones oestrogen and progesterone; *en route*, the ovum (which will eventually form the yolk) is fertilised and surrounded by albumen, membranes and finally a hard calcium shell, which may be coloured by blood and bile pigments. Sequential ovulation and oviposition is unique to birds and may have been an important factor originally favouring the storage of sperm (Birkhead & Møller 1992).

The onset of nesting behaviour is controlled by the endocrine glands, in response to two types of environmental factors: proximate cues (*e.g.* increased daylength, or rainfall in tropical areas), and ultimate factors (*e.g.* food supply, vegetative growth, temperature, competition and predation levels, and the availability of a breeding site or nesting material). The breeding cycle is timed to match fluctuations in the environment, so that chicks hatch when conditions are optimal. When environmental conditions are good, it can be adaptive to telescope the breeding season into a shorter period, to allow the gonads to regress earlier and thereby avoid carrying the extra weight of mature gonads.

It is therefore apparent that the timing of nesting behaviour is fairly flexible, and is adapted to environmental conditions. This observation is supported by Wagner *et al.* (1965), who found a similar adaptability in their study of the ring-necked pheasant *Phasianus colchicus* in Wisconsin (see also Warner RE 1984). A few authors have also reported the phenomenon of several hens depositing eggs in a clutch that was incubated by none of them - a behaviour pattern similar to the dump nesting observed in the Whipsnade population (*e.g.* Mackie &

Buechner 1963; Wagner *et al.* 1965; Heusmann *et al.* 1980). Wagner *et al.* concluded that although the onset of nesting is highly variable, the start of egg laying is relatively fixed, and thus the incidence of dump nesting may vary from year to year. Mackie & Buechner (1963) demonstrated that ovary and oviduct development in the chukar *Alectoris graeca* occurred extremely rapidly prior to the onset of egglaying, which was more synchronous among individuals in their population than the onset of nest building.

The conclusion drawn by Wagner *et al.* could be equally applicable to the peahens at Whipsnade. It is certainly true that at Whipsnade the date of the first viable nest discovered varied from year to year (nesting began on May 19th in 1989, May 9th in 1990, and May 15th in 1991), as did the duration of the nesting season (63 days in 1989, 100 days in 1990, and 75 days in 1991). However, the discovery of the first single egg and dump nest was fairly consistent between years (May 6th and May 5th respectively in 1989, May 3rd and 7th in 1990, and May 8th and 4th in 1991), suggesting that the onset of egg laying may be governed by fixed proximal cues, such as photoperiod or temperature (see Figure 3.6), whereas the timing of nesting behaviour coincides with fluctuations in environmental conditions, such as adequate vegetative nest cover. (These dates refer only to when the first nest of each category was discovered, rather than to when the eggs were actually laid; nevertheless, they do provide an indication of the relative variability of laying dates.) Robinson (1958), Grice & Rodgers (1965) and Heusmann *et al.* (1980) found that the incidence of dump nesting in wood ducks *Aix sponsa* was inversely related to the availability of nest sites. However, this species nests in holes (or artificial nest boxes), and nest sites should not be a limited resource for peahens at Whipsnade.

In the absence of any information about which particular peahens are involved in the deposition of either single eggs or dump nests, I propose that the observed behaviour may be the result of environmental constraints acting upon the population at Whipsnade. The greater variability in the onset of nesting compared with that of non-viable clutches suggests that females may be "compelled" (by an increase in photoperiod, for example) to begin laying by a particular date, perhaps before they have mated or selected a suitable nest site.

Thus single eggs are deposited randomly on the ground, with no effort made to conceal them, since the hen has no intention of incubating them.

However, this does not explain why females should leave eggs in large communal dump nests. Consider the hypothetical situation of a female, obliged by environmental pressures to deposit an egg, but unwilling or unable to make a nest and incubate it. If she then chances across another egg or eggs, it may be more adaptive to parasitise this "clutch" by adding her egg to it, than to abandon her egg where she can be certain it will not be incubated. It is possible that the sight of a clutch of eggs may act as a stimulus to a female to deposit an egg; such unattended nests may also be easier to parasitise simply because they are undefended. Other hens will then follow suit, and so a large dump nest is created. Of course, the attempted parasitism of another hen's clutch can be adaptive only if the egg deposited is fertile. There are no data available on the fertility of abandoned eggs*, but copulations have been observed at Whipsnade from mid-April, and so it is reasonable to assume that dumped eggs need not be infertile.

If hens are obliged by environmental cues to deposit eggs at the start of the breeding season, this does not necessarily account for the larger size of such eggs. Once again, I can merely conjecture about this disparity, but it is possible that hens that intend to parasitise another hen's clutch deposit larger eggs to give the chicks a competitive advantage when they hatch. The occurrence of single abandoned eggs may therefore be the result of females' inability to discover a nest to parasitise before they were compelled to lay an egg.

Since mean egg volume decreases over the breeding season, could abandoned eggs be larger simply because they are laid at the start of the season? This appears unlikely, since they are significantly larger than viable eggs laid at approximately the same time of year (one-tailed t-Test: $n_1 = 38$, $n_2 = 35$, $p = 0.0384$). Alternatively, perhaps not all members of the population are responsible for egg dumping - for example, it may be a strategy of some hens

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* A dump nest of 35 eggs was discovered at Whipsnade in early June 1993, and these were incubated and tested for fertility; 25 were found to be fertile (M. Petrie and T. Burke, pers. comm.).

to attempt nest parasitism before starting to lay and incubate their own clutch (see Section 3.4.2); or young, inexperienced females may be unable to find a suitable nest site before the onset of egg laying. There is however no evidence that young hens lay larger eggs than older females (Figure 3.10*b*).

The strategy of egg dumping observed in the Whipsnade population is certainly intriguing behaviour, but the observations described above provoke more questions than they answer. To gain an insight into why peahens are apparently wasting resources on laying eggs that have no chance of survival, a detailed investigation would be required with close monitoring of all dump nests discovered. One could thereby determine which females are depositing eggs and when, and whether they have started nesting elsewhere or egg dumping occurs before the onset of any nesting activity. If females are already incubating their own clutches, egg dumping would appear to be a misguided attempt at nest parasitism. Abandoned eggs, both singles and dump nests, should also be tested for fertility (see previous footnote), since if the eggs are infertile a hen would gain nothing by depositing it in another clutch, whether incubated or not. Further investigations would thus reveal much about this apparently maladaptive strategy, in particular whether it bears any relation to the nest parasitism described in the following Section.

3.4.2 Nest parasitism at Whipsnade

The care of conspecific young by individuals other than the genetic parent is termed "alloparental care" (Wilson 1975), and in birds it can be further divided into "pre-" and "post-hatch brood amalgamation" (Eadie *et al.* 1988). Post-hatch brood amalgamation (post-HBA), namely the care of unrelated chicks after hatching, will be discussed in detail in Chapters 6 and 7.

Eadie *et al.* (1988) invoked the terms pre-HBA and post-HBA to eliminate some of the difficulties created both by the multitude of names for a single activity, and by the classification of several different behavioural patterns under the same label. For example, the term "dump nesting" has been used to imply the dumping of eggs in large, unincubated clutches (as described in Section 3.4.1), as well as laying eggs in the nest of a conspecific to

avoid the costs of incubation. This latter activity has also been classified in the literature as "egg dumping", "nest parasitism" and "brood parasitism", which can lead to confusion if no formal definition is given. Eadie *et al.* (1988) recommend categorising this behaviour under the broader definition "pre-HBA", although I prefer to use the term "nest parasitism" to describe the particular behaviour pattern observed in the Whipsnade population. In this context, "nest parasitism" indicates the deposition of an egg or eggs by a peahen (the "parasite") in the viable nest of a conspecific female (the "host").

Such intraspecific nest parasitism (INP) is known to occur in up to 200 bird species (Yom-Tov 1980; Møller 1987; Eadie 1991; Lyon 1991, 1993), but detailed studies are relatively rare, notable exceptions being the Hirundinidae (*e.g.* Møller 1987; Brown & Brown 1989, 1991), the Sturnidae (*e.g.* Evans 1988; Pinxten *et al.* 1991), the Rallidae (*e.g.* Lyon 1991; Møller & Petrie 1991; Lyon 1993; Petrie & Hotchin, unpub. ms.) and the Anatidae (*e.g.* Weller 1959; Eadie *et al.* 1988; Semel *et al.* 1988; Eadie 1991).

The majority of species displaying INP are precocial, and the strategy is particularly common amongst the Anseriformes and the Galliformes (Weller 1959; Mackie & Buechner 1963; Yom-Tov 1980; Eadie *et al.* 1988; Rohwer & Freeman 1989; Eadie 1991). For females that feed their young, egg production is a relatively minor component of total reproductive effort (King 1973), and the number of offspring they can raise is generally limited by the time and energy requirements of feeding those young (Lack 1968; Klomp 1970; Ricklefs 1977). In contrast, the brood size of precocial species appears to be constrained mainly by the resources available for egg laying (Lack 1968; Ankney & MacInnes 1978; Drent & Daan 1980; Rockwell *et al.* 1987). This dichotomy led Rohwer & Freeman (1989) to suggest that selection pressure for defence against INP will differ between precocial and altricial species, resulting in the disproportionately higher level of INP among precocial birds.

Precocial species also have relatively larger clutches than altricial species (Ar & Yom-Tov 1978), and incubation generally begins towards the end of the laying period so that the chicks hatch simultaneously. These factors allow a greater length of time, from the onset of laying until the start of incubation, for nest parasites to "sneak in" and deposit a parasitic egg

into the clutch (Yom-Tov 1980). Since many precocial species are also ground-nesters, they may be more susceptible both to nest predation and to INP (Petrie & Hotchin, unpub. ms.).

Until Yom-Tov's (1980) important review, studies of nest parasitism in birds had concentrated on interspecific parasitism - in other words, egg laying by females of one species in the nest of another species (*e.g.* Swynnerton 1918; Friedman 1963; Hamilton & Orians 1965; Rothstein 1971, 1975a,b,c; Payne 1977). Approximately 1% of all bird species are interspecific nest parasites, and unlike species exhibiting INP, the majority have altricial young (Payne 1977; Andersson & Eriksson 1982). The strategy of INP tended to be regarded as something of a reproductive anomaly; parasitic females were thought to be those that had no opportunity to breed themselves, and were thus "making the best of a bad job" (Dawkins 1976; Petrie & Møller 1991). However, it is now widely recognised that INP can be adaptive as an alternative reproductive strategy, involving females which have their own viable nests in addition to parasitising the nests of others.

Adequate investigation of INP within a population ideally requires the identification of parasitic eggs and females, and host females. The occurrence of INP can be detected in several ways:

(a) by direct monitoring of nests. If clutches are observed closely (*e.g.* by auto-triggered or time-lapse photography), the identity of parasitic females and the time of visiting can be recorded. Heusmann *et al.* (1980) identified female wood ducks laying in artificial nest boxes by attaching automatic collaring devices to each box. Frequent inspections of clutch size and individual marking of eggs will reveal whether eggs are appearing outside the host's regular laying sequence, or whether chicks hatch later than the rest of the clutch (Yom-Tov 1980; Brown 1984; Petrie & Møller 1991). Abnormally large clutches may also indicate the presence of parasitic eggs: Yom-Tov (1980) suggests that since the distribution of clutch sizes is normally clumped*, any clutch larger than twice the mean clutch size can be assumed to have been laid by more than one female.

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* Yom-Tov (1980, p. 95) defines a clumped distribution as one in which $\sigma^2 > \mu$ (*i.e.* the variance is greater than the mean). However, I suggest that this inequality is a typographical error, and that it should in fact be $\sigma^2 < \mu$; the former relationship would result in a spread out rather than a clumped distribution. Henceforth the second inequality will be used.

(b) from the individual appearance of the eggs. The degree of variability within and between clutches in the shape, size, colour, patterning and texture of eggs varies between species, and species susceptible to INP tend to exhibit low intra-clutch variation and high inter-clutch variation in these morphological features (Møller & Petrie 1991; Petrie & Hotchin, unpub. ms.). It is argued that a female can recognise a foreign egg in her clutch more easily if the morphology of her own eggs is homogeneous, while deviating markedly from the mean appearance of eggs in the population (Møller & Petrie 1991).

(c) from biochemical or genetical evidence. The techniques of protein gel electrophoresis and DNA fingerprinting are relatively recent developments, allowing the identification of parasitic and host females and eggs (*e.g.* Fleischer 1985; Birkhead *et al.* 1990). To be effective, however, they require that blood samples are taken from all potential nest parasites in a population, which is rarely practical. Nevertheless, they can provide a useful indication of the parasitic eggs in a clutch (Yom-Tov 1980; Petrie & Møller 1991), and, as the techniques are refined, they will undoubtedly shed much light on future research in this area.

(d) from physiological evidence. As described in Section 3.4.1, female birds have a certain number of ova that develop from follicles sequentially over the laying period. Post-ovulatory follicles (POFs) remain in the ovary, and the number of POFs corresponds directly with the number of eggs that have been laid. Thus any discrepancy between a female's clutch size and the number of POFs indicates that she may be either a parasite or a host (Kennedy *et al.* 1989), or have dumped eggs. The major drawback of this method is that females have to be sacrificed for dissection (Petrie & Møller 1991).

Many studies have found that females adopting a parasitic strategy generally fall into four categories: (a) young, inexperienced females, prevented from aquiring a nest site; (b) females that have deserted their nest, through predation or disturbance, food scarcity or bad weather; (c) females in a population with a high density of potential breeders, and hence fierce competition for nest sites; and (d) "professional parasites", females which parasitise the nests of conspecifics in addition to rearing a brood of their own (Yom-Tov 1980; Evans 1988; Eadie 1991; Lyon 1991).

The question of which females act as hosts has received less attention than the identity of nest parasites, but the fitness of a parasite can be greatly influenced by the selection of the host (Friedman 1963; Payne 1977; Fleischer 1985). The cost to a female of selecting a low quality host is that she may decrease her own overall reproductive success, if the parasitic eggs or chicks receive inadequate care (Rothstein 1976a; Middleton 1977), whereas a female choosing a high quality host may suffer rejection of her eggs or chicks (Rothstein 1976a,b, 1982; Scott 1977).

Nest parasitism can be regarded as the outcome of an evolutionary "arms race" between host and parasite (Dawkins & Krebs 1978; Andersson 1984; May *et al.* 1991; Petrie & Møller 1991). Little empirical work has been done on the effects of parasitism on the reproductive success of either party (Pinxten *et al.* 1991); indeed, one of the reasons why INP was viewed as "making the best of a bad job" was that the hatching success of parasitic eggs is frequently much lower than that of non-parasitic eggs (*e.g.* Evans 1988). Hamilton & Orians (1965) believed that in order for nest parasitism to be successful, a parasitic egg must have a high probability of fledging. This view however disregards the fact that many nest parasites also have their own nest, and the reproductive success of such a mixed strategy is often greater than that of being a non-parasite (*e.g.* Møller 1987; Brown & Brown 1989; Eadie 1991; Lyon 1991).

Costs and benefits

Individuals may benefit from parasitising the nests of conspecifics if the cost of producing eggs is relatively low compared with the cost of incubation or caring for chicks, and the parasites are therefore able to exploit the host's parental care (Petrie & Møller 1991). This reduction in the fitness costs of parental expenditure may allow the parasite to increase the number of eggs she produces overall in a season (Heusmann *et al.* 1980), or defer the investment to subsequent years, thereby increasing the number of potential breeding attempts (Eadie 1991). Young or inexperienced females may improve the parental care of their offspring by parasitising the nests of older females (Eadie 1991). The deposition of eggs in several nests also spreads the risk of predation, thereby increasing the chance that at least

some of them will fledge, as well as reducing sibling competition (Payne 1977; Brown & Brown 1989; Petrie & Møller 1991).

The main fitness cost to the host is the care of unrelated offspring. This cost may be reduced if the parasites are related to the host, for example in populations with a high degree of female philopatry, in which case the host can contribute to its inclusive fitness by accepting foreign eggs. However, the addition of parasitic eggs to a clutch may make it more visible to a predator, or increase intra-brood competition. It can also reduce the efficiency of incubation, for example if the eggs are not adequately covered by the brood patch, and incur metabolic costs: Smith (1989) showed that larger clutches take longer to incubate, and require more rewarming. Females may respond by producing smaller clutches as an insurance against the crowding effects of INP, which can reduce their own reproductive success (Andersson & Eriksson 1984; Power *et al.* 1989; Pinxten *et al.* 1991; Yamauchi 1993). If a female deserts her nest completely, her reproductive success for that season may be nil if she is unable to renest (Petrie & Møller 1991).

Tactics of parasites

Nest parasitism can thus be an adaptive strategy, but certain conditions and tactics adopted by parasites can further enhance its success. The success of parasitic eggs is greater in the following circumstances:

(a) When eggs are laid synchronously with the host's clutch, particularly during the early part of the laying period (Andersson & Eriksson 1982; Møller 1987; Evans 1988; Brown & Brown 1989). Eggs laid too early are often rejected by the host, and eggs laid late will hatch late; this is particularly important in nidifugous species, in which the brood leaves the nest almost immediately after hatching, and any unhatched eggs will be abandoned.

(b) By depositing only one or two eggs in a host's nest, and opting for relatively large host clutches, the parasitic egg(s) will form a lower proportion of the total clutch, and the host is less likely to desert (Yom-Tov 1980; Andersson & Eriksson 1982; Evans 1988; Pinxten *et al.* 1991; Petrie & Hotchin, unpub. ms.). This favours the distribution of parasitic eggs between nests, so that parasites are not specific to particular hosts (Evans 1988).

(c) In some species, parasitic females remove one of the host's eggs before depositing their own, so that clutch size remains constant (*e.g.* Pinxten *et al.* 1991). Again, this tactic can reduce the likelihood that the nest is abandoned.

(d) Parasitism is more prevalent when nests are closely spaced. In many colonial species, parasitic eggs are laid by neighbouring females, and the degree of parasitism is correlated with colony size, up to a certain threshold (Møller 1987; Brown & Brown 1989). Parasitic females may even spend time actively searching for unattended nests (Pinxten *et al.* 1991).

Tactics of hosts

Potential hosts in species with INP have evolved several strategies to combat parasitism:

(a) Nest guarding and aggression can serve to deter intruders (Møller 1987) and should theoretically be greatest when the nest is most at risk (Petrie & Møller 1991).

(b) If a host can recognise the presence of an alien egg in her nest, she is then able to eject it and thereby avoid the costs of incubating it (Møller & Petrie 1991; Pinxten *et al.* 1991). Females can increase the chance of detecting foreign eggs by decreasing the variability of egg appearance in their own clutch, and by making their own eggs very different from the population mean (Møller & Petrie 1991; Petrie & Hotchin, unpub. ms.). However, host females may accept rather than reject alien eggs, for several reasons (Møller & Petrie 1991): for example, if host and parasite are related (Andersson & Eriksson 1982; Andersson 1984); if there is some benefit to the host, such as predator dilution (Eadie & Lumsden 1985); if the host is forced to accept by the risk of nest destruction (Zahavi 1979); or if there is a danger of ejecting their own egg by mistake (Weller 1959; Arnold 1987; Eadie *et al.* 1988).

(c) Since the most likely parasites are neighbouring females, a potential host can reduce the risk of INP by nesting asynchronously to her neighbours (Møller & Petrie 1991).

(d) A female may respond to extreme levels of parasitism by resorting to nest desertion (Andersson & Eriksson 1982).

Parasites with their own nests are also at risk of being parasitised themselves, when they are away from the nest. The most successful method of avoiding this danger appears to be to adopt the two alternative reproductive strategies at different times (Petrie & Møller 1991). Parasites commonly parasitise other clutches early in the season, and then make their own nest which they can defend against intruders (Lyon 1991; Petrie & Hotchin, unpub. ms.).

Nest parasitism at Whipsnade

The identification of parasitised nests at Whipsnade was difficult, since many of the methods suggested above could not be used. Identification of parasitic hens was not possible, since the only females seen at viable nests (apart from one) appeared to be responsible for their incubation. The one exception was when a ringed female was flushed from a nest containing six eggs, which was known to have been incubated for three days by an unringed female. The nest eventually contained twelve eggs, five of which hatched.

I found that peahens at Whipsnade generally lay eggs in the afternoon of every other day, but occasionally eggs appeared on the days in between, or up to a week after the clutch was apparently complete. Hens begin to sit on the nest from around the fourth or fifth egg, even when the final clutch size is larger; since peachicks hatch synchronously, it is possible that females are not actually incubating the clutch from the start, but are sitting on the nest as a protection against INP. Several females were observed "loitering" within the vicinity of their own nests, after the onset of egglaying but before the start of incubation, and these hens may have been performing some kind of nest-guarding behaviour.

Physiological evidence of egglaying was not obtainable from the peahens at Whipsnade, since the necessary dissections would have made subsequent observation of their behaviour rather difficult. However, DNA fingerprinting may in the future provide some biochemical indication of nest parasitism in the population. Blood was extracted from many of the females at the time of capture, and from all chicks caught; I also dissected all unhatched eggs remaining in the nest after a hen had removed her brood. Both blood samples and any resulting embryos were sent away for analysis to Terry Burke and Olivier Hanotte at

Leicester University, and their work may yield some interesting data on the prevalence of pre- and post-HBA at Whipsnade, but at the time of writing no information is yet available.

Identification of INP thus relied on the existence of abnormally large clutch sizes, the appearance of eggs outside the host's regular laying sequence, and nests containing eggs which differed markedly in shape, size and appearance. Eggs which remained unhatched after the female had left the nest provided some indication that they may have been laid after the host hen had completed laying. Yom-Tov (1980) suggests that clutches more than twice the mean clutch size can be assumed to contain parasitic eggs, but there were relatively few such large clutches. Table 3.2 shows that over the three study years the mean viable clutch size was 4.885 ± 2.327, which approximates to a clumped distribution (*i.e.* $[2.327]^2$ = 5.415)*. Since the mean is roughly twice the value of the standard deviation, 2μ (= 9.77 eggs) approximates to $\mu + 2\sigma$ (= 9.54 eggs), and there were only three viable clutches of ten or more eggs. If the definition of "abnormally large" is extended to include clutch sizes equivalent to $\mu + \sigma$ (= 7.21 eggs), there were nine such nests in total (clutch sizes were 7, 8, 8, 8, 9, 9, 10, 12, and 12).

The colour of peahens' eggs varies from a creamy white to a pale buff brown, and may be plain or brown-speckled to various degrees (Plate 3.5). Some shells are extremely smooth, while others appear more porous and almost rough to the touch. Photographs were taken of the marked eggs in every clutch (Section 2.3.2), and these were used to investigate intra-clutch variation in egg appearance (Plate 3.6). The photographs were presented independently to five people, who classified each clutch according to the criteria given on page 123.

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* If the data from 1991, which had rather large clutch sizes, are removed, mean viable clutch size becomes 4.588 ± 1.848, which fulfills the requirements of the inequality (*i.e.* $[1.848]^2 = 3.415 < 4.588$); similarly, within each year clutch sizes tend to form clumped distributions (1989: $[1.76]^2 = 3.098 < 4.33$; 1990: $[1.91]^2 = 3.648 < 4.77$; and 1991: $[2.62]^2 = 6.864 \approx 6.40$).

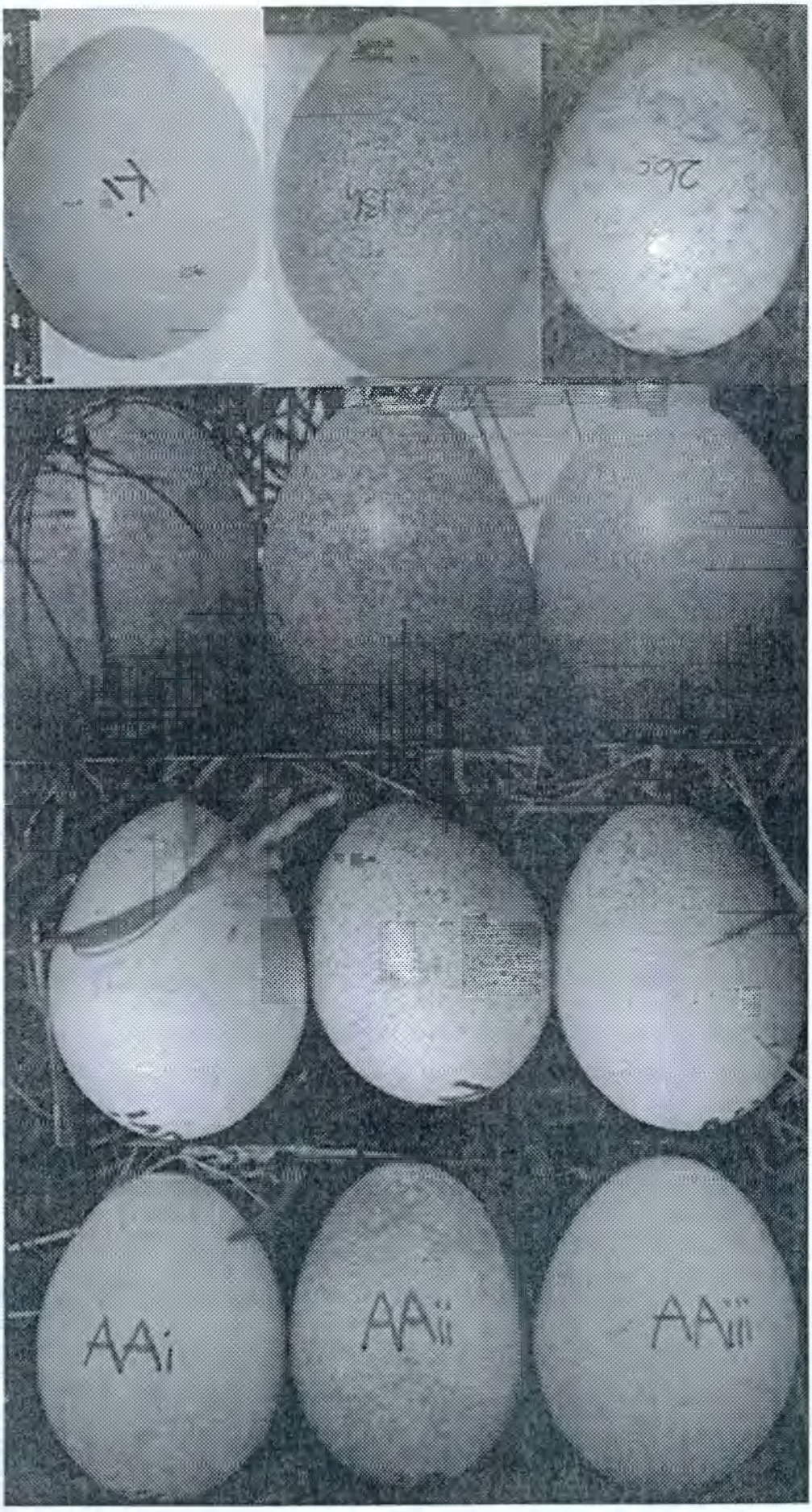


Plate 3.5. Natural variation in the size, shape and appearance of peahen eggs.

Category 1: No variation in egg appearance throughout the entire clutch;

Category 2: Some eggs differed in appearance from the majority of the clutch, with regard to colour, texture or patterning (records were also made of any of these "odd" eggs that appeared similar to each other).

Consistency between the five people's responses was tested for each clutch using the Kendall coefficient of concordance, and there were no significant differences.

Plate 3.6. Clutch classified as containing a parasitic egg (lower right). The other four eggs were all similar in appearance in the original colour photograph; two of the eggs appear darker here because they were discoloured by dirt.

It has previously been shown (Figure 3.13) that individual hens seem to be fairly consistent in the size of eggs they produce, so eggs that lie outside this range may indicate that INP has occurred. The threshold for deciding whether a particular egg is an outlier is that it is > $10cm^3$ larger or smaller than the mean intra-clutch egg volume. Variation in egg shape was assessed using the ratio of length to width, and the shape of all eggs from viable nests is shown in Figure 3.23. It can be seen that there is considerable variation in egg shape within the population, and that eggs defined as parasitic (see Table 3.5) do not appear to differ from non-parasitic eggs. Individual females tend to produce eggs of a similar shape, even if they differ slightly in size (*i.e.* when length is plotted against width, eggs generally lie along a straight line with a positive gradient), and outlier eggs of a different shape can be assigned as potentially parasitic. Figure 3.24 illustrates the difference in plots between nests with and without an outlier, and a known dump nest is also plotted to show the variation in egg shape produced by different hens.

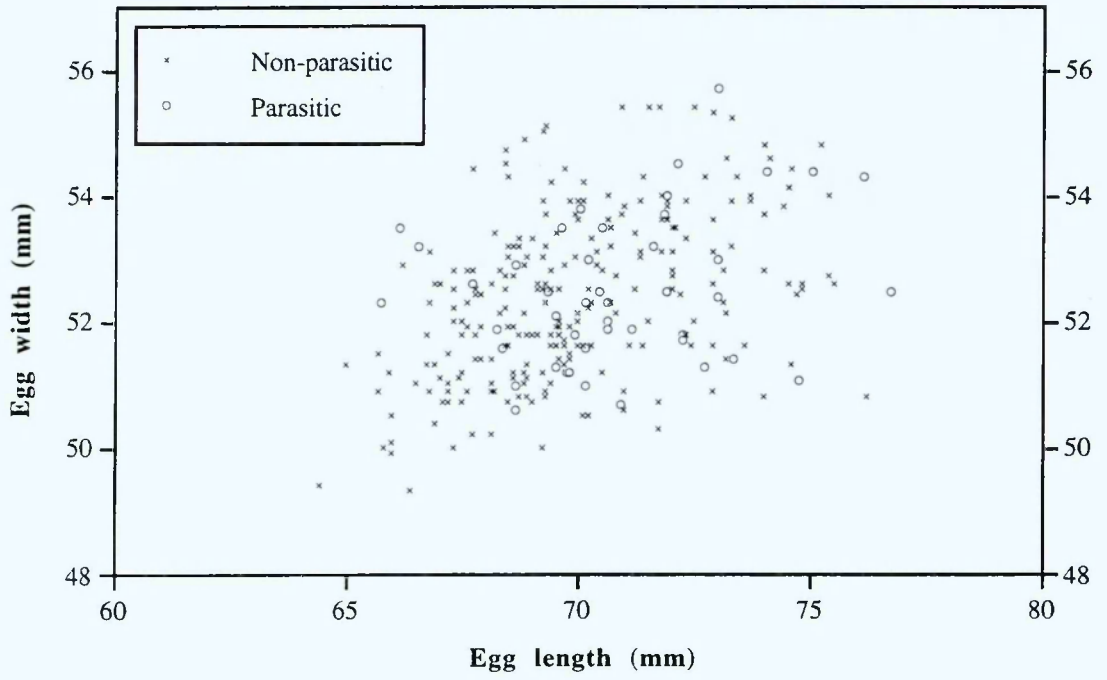


Figure 3.23. Variation in egg shape of parasitic and non-parasitic eggs found in all viable nests.

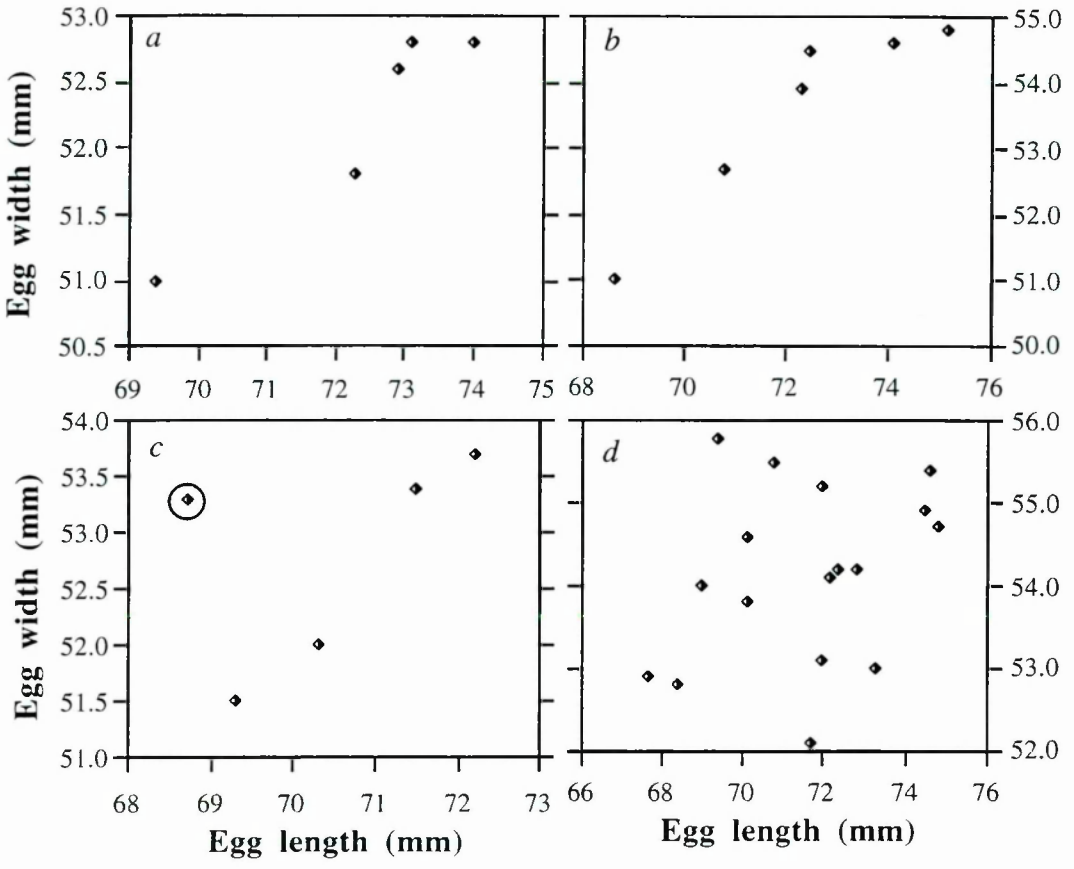


Figure 3.24. Intra-clutch variation in egg shape for individual nests. *a,b:* Nests with no obvious outliers. *c:* Nest containing one egg of a different shape (circled); INP suspected. *d:* Egg shapes of a dump nest, laid by several hens.

Of the 61 viable nests discovered over the three study years, 59 were photographed; 35 fell into Category 1 - *i.e.* no nest parasitism suspected, and 24 fell into Category 2. For all nests, records were also made of any unhatched eggs, and of any eggs which appeared more than two days after the hen had started incubation, but there were too few data available on eggs laid between the owner's regular laying sequence to be useful. All unhatched eggs were dissected, and those that proved infertile were discarded from the analyses (only two such eggs were found). Details of nests suspected of containing one or more parasitic eggs are shown in Table 3.5. Eggs bracketed together refer to those that were similar to each other (and may have been laid by the same nest parasite). An egg was defined as parasitic if it occurred in two or more of the five discriminatory categories.

Nest details		Outlier eggs			Egg timers		Identification	
Nest	Clutch size	Appear-ance	Size	Shape	"Late" eggs	Unhatch-ed eggs	Parasitic eggs	% clutch parasitic
A	6	f		f	f	(Predated)	f	16.67
B	6		f		f	(Deserted)	f	16.67
C	8	f	c,f	c	f,g,h	b,c,d,f	c,f	25.00
D	6	e		e		c,e	e	16.67
E	7	[f,g]		g	f,g	(Deserted)	f,g	28.57
F	12	h,k,[j,l]	k,l	h,j,l	g,h,i,j,k,l	a,f,g,h,k,l	g,h,j,k,l	41.67
G	10	j		b	h,j	b,c,d,i,j	b,j	20.00
H	6	c,f	c,e	c		b	c	33.33
I	9	h,i		h	h,i	a,b,c,d,h,i	h,i	22.22
J	5			e	d,e	e	e	20.00
K	6	a	a			(Predated)	a	16.67
L	6		c			c	c	16.67
M	8	c,g		g	g,h	a,d,g	g	12.50
N	4	d				d	d	25.00
O	6	d		d		c,d,f	d	16.67
P	4	a	a	a		–	a	25.00
Q	5	d	d			b,d,e	d	20.00
R	5	a		a		a	a	20.00
S	5	d,e				d	d	20.00
T	5			e	d,e	–	e	20.00
U	12	[d,i]	d	g,[d,i]	g,h,i	(Deserted)	d,g,i	25.00
V	8	f		f	e,f,g,h	a,b,d,f	f	12.50
W	9	[a,i]	[a,i]		i	b,c,f,g,i	a,i	22.22
X	7		g	g		a,d,g	g	14.29

Table 3.5. Assignment of eggs into various categories, according to egg morphology and timing. Eggs which occur in two or more of the discriminatory categories are defined as parasitic (for details, refer to text). The 24 clutches here represent the parasitised clutches over all three years of study, and are arbritrarily renamed A to X.

Twenty four of the 61 viable nests discovered (= 39.34%) were suspected of containing parasitic eggs, and 35 of the 298 eggs found (= 11.74%) were defined as parasitic. It is possible that the discriminatory methods used underestimate the true frequency of INP in the Whipsnade population, but hopefully the use of five separate analyses of outliers will minimise this risk.

Table 3.5 shows that very few nests suspected of being parasitised contained more than two eggs which differed markedly in appearance from the rest of the clutch, and in only four cases were two parasitic eggs similar to each other. If hens do lay eggs which are consistent in appearance, then these data suggest that parasitic females are not generally parasitising host clutches more than once. The mean overall viable clutch size is 4.885 (Table 3.2), and the mean size of clutches suspected of being parasitised is 6.875; thus INP apparently increases clutch size by approximately two eggs. However, the mean number of parasitic

eggs per parasitised clutch is only 1.458, so peahens may be selectively parasitising the larger clutches.

If those eggs identified as parasitic are removed from the analysis, the resulting clutch size should represent the size of the host clutch before parasitism. Figure 3.25 shows that there is a highly significant relationship between clutch size and susceptibility to parasitism.

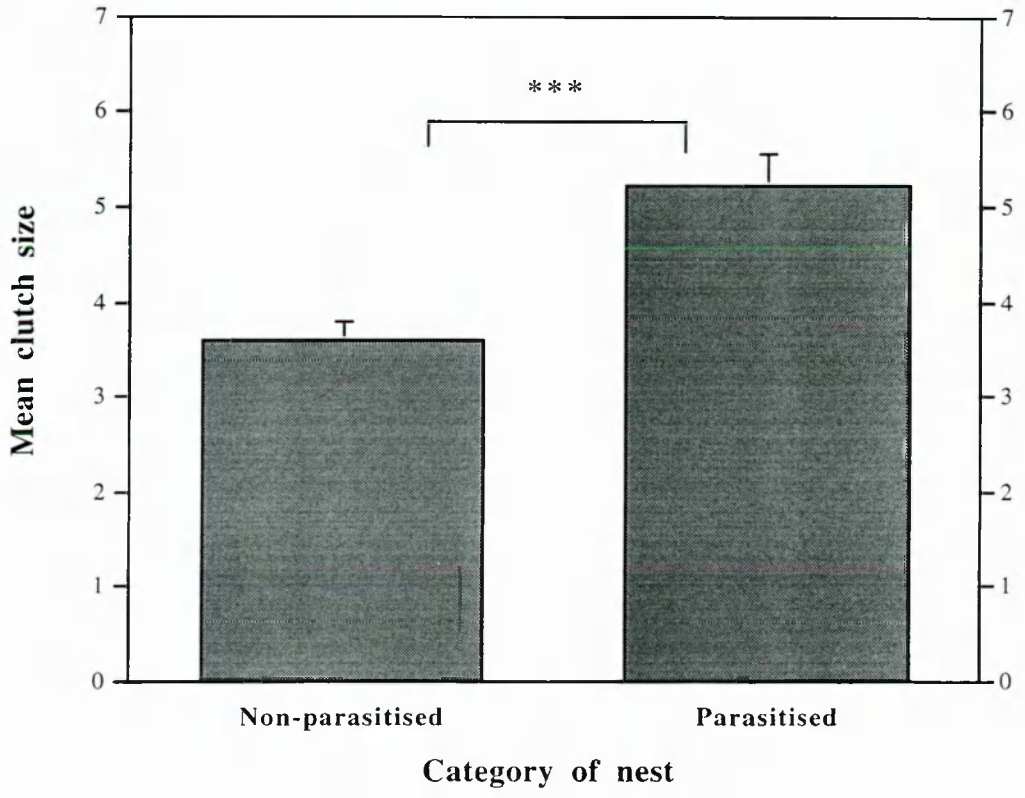


Figure 3.25. Mean clutch size of non-parasitised and parasitised nests. Sizes refer to the size of the host's clutch *before* parasitism. Data were compared using the Mann-Whitney U test: $n_1 = 35$, $n_2 = 24$, $p < 0.00003$.

Taking the 24 clutches described in Table 3.5, the mean egg volume of those eggs identified as parasitic was greater (though not significantly) than that of the host eggs in the clutch (Figure 3.26). However, if we consider all 59 viable clutches, Figure 3.27 demonstrates that the mean egg volume of parasitised clutches is significantly greater than that of non-parasitised clutches. This suggests that parasitic females may be selectively parasitising not only larger clutches, but also those containing larger eggs.

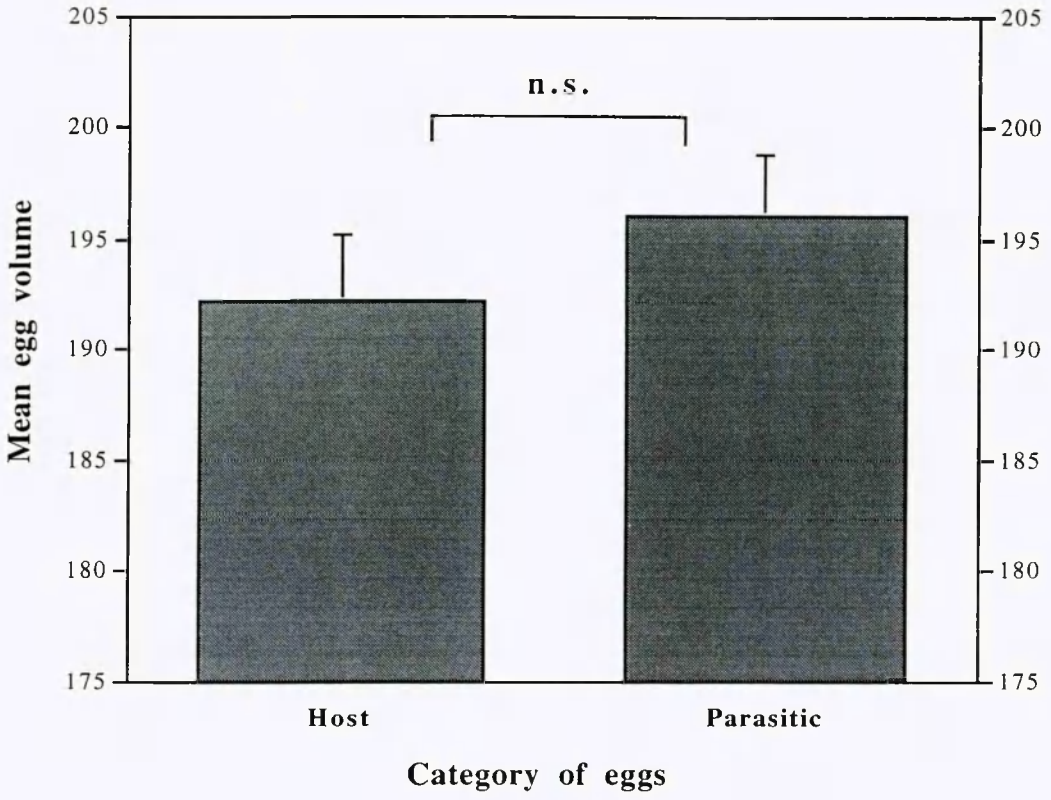


Figure 3.26. Mean egg volume (cm^3) of host and parasitic eggs within parasitised clutches. Bars represent standard error of the mean. Data were compared using a paired t-Test: $n_1 = n_2 = 24$, $p = 0.1423$.

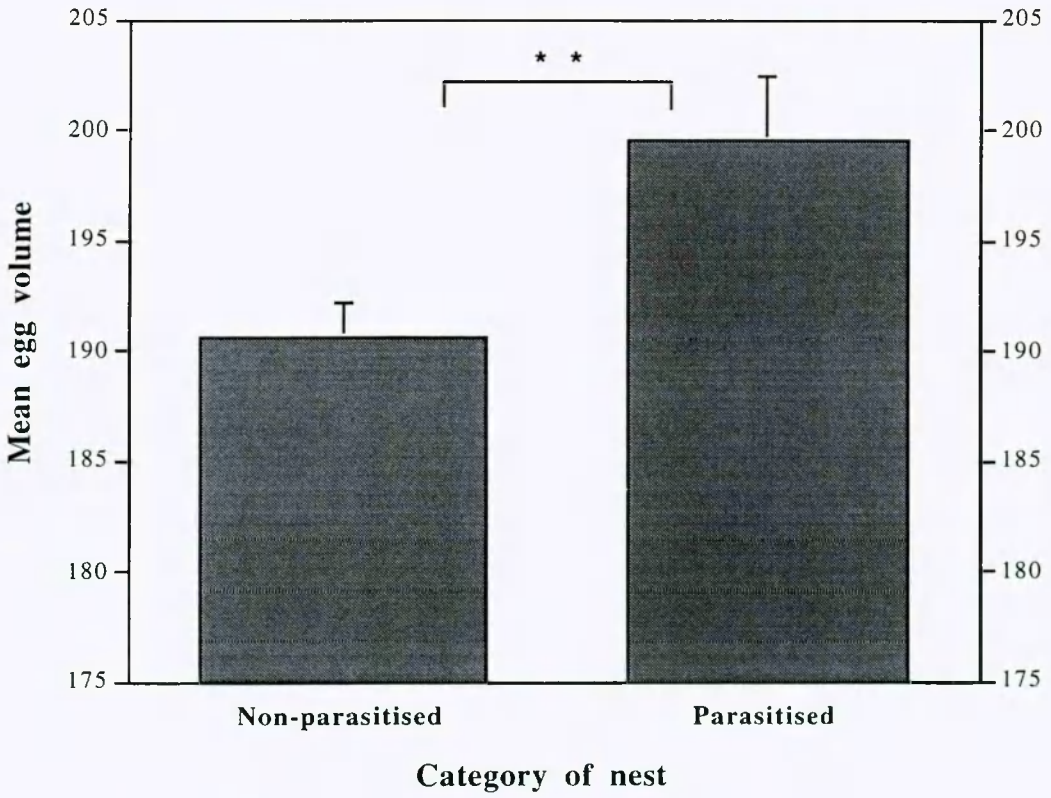


Figure 3.27. Mean intra-clutch egg volume (cm^3) of non-parasitised and parasitised nests. Bars represent standard error of the mean. Data were compared using a Mann Whitney U test: $n_1 = 24$, $n_2 = 35$, $p = 0.0096$.

Parasitised nests occur significantly earlier in the breeding season than non-parasitised nests (Figure 3.28). However, since both clutch size and mean intra-clutch egg volume are significantly correlated with laying date (Figures 3.3 and 3.4), it is not clear which factor (egg volume, clutch size or date of lay) may be most important in deciding which clutches are most susceptible to INP. Stepwise regression analysis was therefore used to determine the relative importance of these parameters for the manifestation of nest parasitism (Table 3.6).

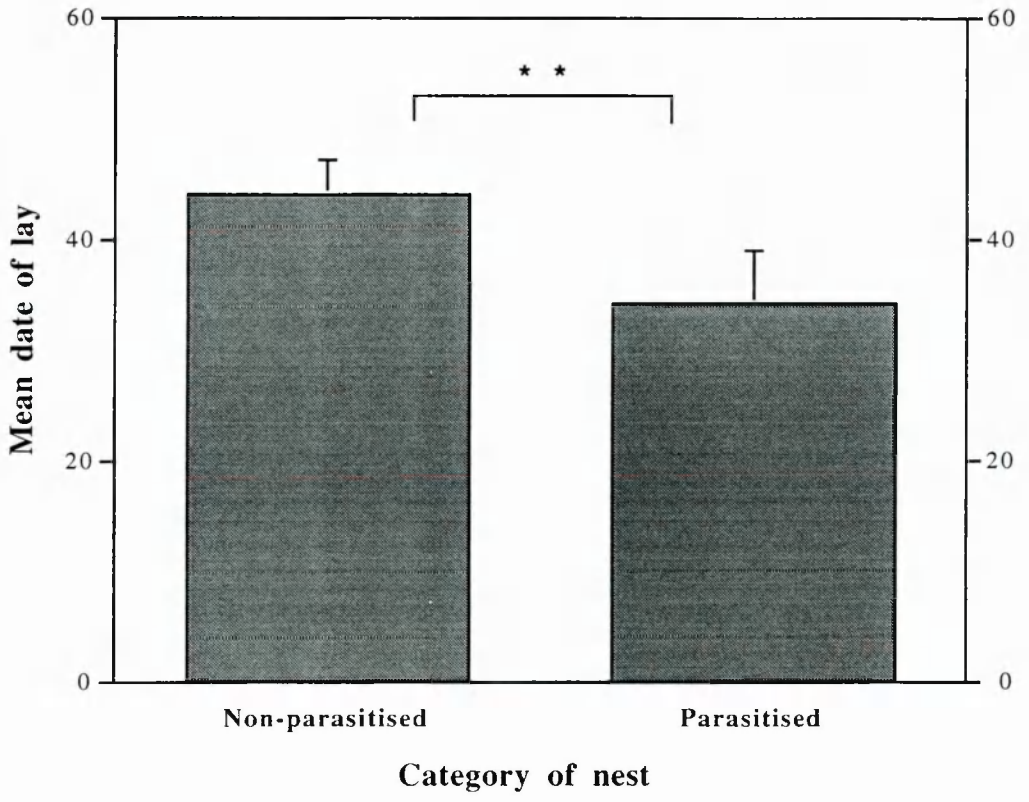


Figure 3.28. Mean laying date (in May days) of parasitised and non-parasitised viable clutches. Bars represent standard error of the mean. Data were compared using a Mann-Whitney U test: $n_1 = 24$, $n_2 = 35$, $p = 0.0022$.

Table 3.6 demonstrates that among the population at Whipsnade, variation in INP (*i.e.* whether or not a nest is parasitised) can be explained almost entirely by variation in the potential host's clutch size - in other words, larger clutches are more likely to be parasitised than smaller ones, irrespective of the host's mean egg volume, or the date of lay. It is possible that parasites are selectively laying eggs in larger clutches, since their egg will then form a lower proportion of the total clutch and the host is less likely to reject the parasitic

Parasitism equation	Host clutch size	Host mean egg volume	Date of lay (May days)	Intercept	Significance of equation
(i) Coefficients	0.1293	0.0072	0.0006	−1.6011	
p =	*0.00006*	*0.19833*	*0.86159*	*0.16080*	*0.00005*
(ii) Coefficients	0.1270	0.0068		−1.4966	
p =	*0.00001*	*0.18162*		*0.11985*	*0.00001*
(iii) Coefficients	0.1333			−0.2264	
p =	*0.000004*			*0.08278*	***0.000004***

Table 3.6. Stepwise multiple regression analysis of host clutch parameters in relation to whether a nest is parasitised or not. Multiple regression equations are calculated (i) for all variables recorded (host clutch size and mean egg volume [both measured before the addition of parasitic eggs], and laying date); (ii) for clutch size and egg volume; and (iii) for clutch size only. P values are given for each of the coefficients, and for the whole regression equation.

egg. Alternatively, since larger clutches take longer to lay, and peahens do not begin incubation until laying is complete (or nearly complete), there will be increased opportunity for females to parasitise larger clutches. Andersson (1984) proposed that this trait might partly account for the high frequency of INP in waterfowl, and Eadie's (1991) phylogenetic analysis of INP in the Anatidae similarly showed that parasitic species have larger clutches and longer laying periods than non-parasitic species.

Further analysis is therefore needed to determine whether large clutches are parasitised preferentially, or simply because of the greater opportunities for parasitism during the laying period. This "risk period" is obviously proportional to overall clutch size, but since hens do not generally start incubation later than the fifth or sixth egg, I have assumed that the risk period will be constant for clutches of six or more eggs. The risk period for clutches of up to five eggs is calculated using the formula [(2 x clutch size) – 3] days; for clutches of six or more, the period is estimated to be eight days. Given that clutch size is important, multiple regression analysis can then be performed to determine which of the two clutch variables (clutch size and risk period) is a better predictor of whether a nest is parasitised or not (Table 3.7).

Parasitism equation	Host clutch size	Host risk period	Intercept	Significance of equation
(i) Coefficients	0.0528	0.0964	–0.4110	
p =	*0.19098*	*0.01218*	*0.00120*	1.499×10^{-8}
(ii) Coefficients		0.1381	–0.38386	
p =		3.718×10^{-9}	*0.00218*	$\mathbf{4.009 \times 10^{-9}}$

Table 3.7. Stepwise multiple regression analysis of intraspecific nest parasitism with respect to host clutch size and risk period (*i.e.* laying period before the onset of incubation, when the nest is not attended). Multiple regression equations are calculated (i) for both clutch size and risk period, and (ii) for risk period only. P values are given for each of the coefficients, and for the whole regression equation.

Multiple regression analysis (Table 3.7) reveals that the apparent relationship between clutch size and INP is much more likely to be due to the duration of the laying period, rather than to clutch size *per se*. Females do not therefore seem to be selectively seeking out large clutches in which to dump eggs; in contrast, the parasitism of larger clutches appears to be a result of the greater probability of discovering a large nest before the onset of incubation, compared with smaller nests.

Although the date of lay does not explain a significant amount of the variation in INP (Table 3.6), nevertheless Figure 3.28 shows that nest parasitism is more likely to occur earlier in the season. It has been argued (Møller & Petrie 1991; Petrie & Hotchin, unpub. ms.) that within species susceptible to INP, variation in egg size, shape and appearance *between* clutches is often greater than variation *within* clutches, to maximise the chances of host females detecting a foreign egg. This was supported to a certain extent by the data from the Whipsnade population, particularly with respect to egg volume (Figure 3.13). One might therefore expect intra-clutch variation to be lower at the start of the season, when the risk of being parasitised is greatest, and to increase over the season as the risk diminishes. However, the degree of intra-clutch variation (measured by the coefficient of variation) did not change significantly over the season in any of the variables measured, suggesting that the benefits of maintaining a high consistency in egg characteristics may not be sufficiently large to necessitate an increase when the risks are greatest.

There is additionally little evidence that peahens eject parasitic eggs, even if they do recognise them. Why should females accept foreign eggs into their clutch, thereby incurring the costs of incubation with no increase to their inclusive fitness? Several studies of precocial species indicate that females are capable of raising more chicks than the number of eggs they lay (the cost of caring for a precocial brood is often considerably lower than the cost of feeding an altricial brood), and it has been suggested that females are laying less than their maximum clutch size in order to allow room for potential parasitic eggs (Rohwer 1984; Eadie *et al.* 1991).

This tactic would seem to be adaptive only if there are costs of rejecting parasitic eggs, or if there is some advantage to be gained from acceptance (Yamauchi 1993). I suggest that, given the relatively large size of peahen clutches, the cost of accepting alien eggs may be lower than the risk of ejecting a host egg. Possible advantages of INP to the host have been discussed above, and an important factor could be the predator dilution effect. By caring for alien eggs, and subsequently chicks, a hen can reduce the risk that one of her own chicks is taken (see Chapter Six). The mortality rate of peachicks at Whipsnade is very high, and potential predator dilution may justify the acceptance of parasitic eggs.

A discrepancy in the hatching success of parasitic and non-parasitic eggs may also justify the acceptance of foreign eggs (all other things being equal), if parasitic eggs are much less likely to hatch than host eggs, since the resulting brood size would consist predominantly of the host's own offspring. Mean hatching success of non-parasitised, host and parasitic clutches is given in Table 3.8. These data include only those viable clutches of which at least a proportion hatched, and does not take into account deserted or predated clutches. Viable nests are separated into parasitised and non-parasitised nests; parasitised nests are further divided into "host" and "parasitic" clutches, but a single parasitised nest will consist of one "host" clutch and one "parasitic" clutch.

Category of clutch	Total no. nests	Total no. eggs	Mean clutch size	Total successful nests	Total eggs from successful nests	Total eggs hatched	% eggs hatched	Chicks per clutch
All viable nests	61	298	4.885	49	235	163	69.36	3.39
Non-parasitised nests	37	133	3.605	30	107	82	76.64	2.76
Parasitised nests	24	165	6.875	19	128	81	63.28	4.35
Host clutches	24	130	5.417	19	101	74	73.27	3.97
Parasitic clutches	24	35	1.458	19	27	7	25.93	0.38

Table 3.8. Hatching success of parasitised and non-parasitised nests. "Successful nests" refers to the subset of each category from which some eggs hatched (*i.e.* abandoned and predated clutches are omitted).

The results shown in Table 3.8 illustrate the difference in clutch size between nests that are parasitised and those that are not (6.875 *vs.* 3.605). The hatching success of host females is lower than that of non-parasitised females (73.27% *vs.* 76.64%), but because of their much larger clutch sizes host females produce more than one extra chick per nest than non-parasitised females (3.97 *vs.* 2.76). The percentage of parasitic eggs hatched is only about a third of the proportion of non-parasitic eggs hatched, and parasitic eggs give rise to only 4.49% of all chicks produced. Since chicks could not be marked in the egg (unlike the coot *Fulica americana* chicks in Lyon's (1993) study), and the results of blood tests are unavailable, relative post-hatching success of parasitic and non-parasitic chicks cannot be determined.

At first sight nest parasitism does not appear to be a beneficial strategy for peahens at Whipsnade, and one might therefore conclude that hens are making the best of a bad job. However, if parasitic females also have their own nests, INP can still be an adaptive strategy, since evolution will select for even a slight increase in the total number of chicks produced. It is difficult to determine the cost of INP to the host, since host clutches hatch even more chicks per nest than non-parasitic nests. Straightforward comparison is not

meaningful, since host clutches are significantly larger to begin with, and there may be additional confounding effects such as female quality.

As explained above, the identity of parasitic females could not be determined in the present study; however, the majority of hosts can be identified. Petrie & Hotchin (unpub. manus.) found in moorhens *Gallinula chloropus* that lighter females are more at risk from parasitism, but there is no evidence from the population at Whipsnade that host peahens differ greatly in weight or condition from unparasitised females (Chi-squared test: $p = 0.4016$). However, the limited data on female age suggest that younger hens are more likely to be parasitised than older females, although the result is not significant (Chi-squared test: $p = 0.1521$). This contrasts with the prediction previously introduced, that young, inexperienced females can benefit from being a parasite by exploiting the nesting experience of older hens (Payne 1977; Rothstein 1976a,b, 1982; Fleischer 1985; Eadie 1991).

It has been demonstrated that older females nest significantly later in the season than young hens (Figure 3.9*c*), and are parasitised less. Since most of the cases of INP were observed at the start of the season (Figure 3.27), it appears likely that older females may be responsible for parasitising the nests of young hens, and may be delaying their own nesting attempts in order to reduce the risk of being parasitised themselves. Even though an inexperienced female may not be able to provide the same quality of parental care as an older hen, it would still be adaptive for a female to leave her egg in the care of a younger hen rather than incubate it herself, since the cost of laying an egg is considerably lower than the cost of raising that offspring to independence (Clutton-Brock 1988).

In conclusion, I suggest that nest parasitism may have evolved as a mixed strategy, with hens opportunistically parasitising the nests of conspecifics prior to incubating their own clutch, thereby increasing their overall reproductive success. However, without accurate identification of parasitic females and eggs, the full extent of INP at Whipsnade, and its causes and functions, cannot be determined. It is also important to establish the relative reproductive success of parasitic, non-parasitic, and host peahens in order to find out how adaptive the strategy is.

3.5 Intra- and interspecific interactions

In this section, I present a few observations of the interactions of nesting peahens both with conspecifics and with other species. When females are attending a clutch, they are necessarily confined to a particular location for much of the time, and are thus susceptible to the attentions of other individuals.

Peahens usually make their nests in isolated sites, some distance from the main feeding, roosting and loafing areas of the rest of the population, and other males and females would not therefore generally be found anywhere near the nest. Incubating females leave the nest about twice a day to feed, usually for no longer than 10-15 minutes, and then hurry back to the nest. These hens are distinguishable from non-incubating females by their bedraggled appearance, raised neck feathers, and the haste with which they march to and from the nest. If they are so easily recognisable by a human observer, it is likely that other individuals can similarly detect that a particular peahen is nesting.

Other peahens appear to have few interactions with nesting females, apart from when they coincide at a feeding site. Similarly, territorial males generally remain on their lek display sites except when feeding, and have little to do with nesting hens.

The same is not true for non-territorial males. Juvenile peacocks, usually two year olds but occasionally one year olds, and "floaters" were seen on many occasions following a female back to her nest; sometimes there would be as many as three males pursuing a single hen. Males were never observed following other non-incubating females, but very occasionally a young male was observed following a hen with a newly hatched brood of chicks.

Male-female interactions were not limited to when the female was hurrying between nest and feeding site. During my time-budget observations of incubating hens, I saw several instances of males (usually two year olds) approaching a sitting hen at the nest. They would circle around the female, sometimes for twenty minutes or more; on three occasions I also saw males severely harassing a hen (Plate 3.5). This harassment took the form of rushing at the female, pecking at her head and body, and treading her back; one two year old male

twice mounted, and appeared to attempt copulation with, a hen as she tried to roll her eggs. When she stood to defend herself, the males would also peck at her eggs in the nest. This phenomenon is apparently not unique: Goldsmith (1774) suggests that peahens nest under thick undergrowth primarily not for protection against predators, but to hide the nest from males, "who would otherwise disturb her sitting, and break her eggs". Males were never observed attacking abandoned eggs in such a way.

Plate 3.7. Two 2-year-old males "harassing" an incubating female.

It is difficult to determine why particular males should devote so much attention, and even aggression, to nesting females. The males involved were either juveniles or adult floaters, and there is no evidence that non-territorial males such as these ever achieved a successful copulation with any female, although floating males often attempted to mate with a female by intercepting the courtship of a lek male (M. Petrie, pers. comm.). The males involved in the behaviour pattern described above would therefore be certain that they had not copulated with any nesting hen, and could not be the father of any of her eggs.

I suggest therefore that males are able to detect whether a particular female has a nest - perhaps from her appearance, or some olfactory cue - and attempt to force her to abandon

her clutch by harassing and attacking her. They may then gain the opportunity to mate with her, even attempting to "rape" her at the nest, in order to achieve some reproductive success in that season. There is some evidence that males may be sexually mature at two years old, although not having developed the full secondary sexual characters of a mature cock (R. Thornhill, pers. comm.). If this is indeed the function of the observed behaviour pattern, it is akin to the strategy employed by male African lions taking over a new pride: the new male coalition kills any existing cubs (to which they are not related), thereby speeding up the lionesses' return to sexual receptivity (Bertram 1975; Packer & Pusey 1984; Packer *et al.* 1988).

Interactions of nesting hens with other species have seldom been observed, although one or two deserve particular mention. Most other mammals and birds approaching a female on the nest are ignored by her, unless the individual is a potential threat to her or her clutch. Known predators of peahen eggs at Whipsnade include crows, magpies, and a few mammals (see Section 1.1.3), and one notable interaction was between an "old" peahen (at least five or six years old) and a magpie *Pica pica*. The magpie approached the nest on foot, towards the rear of the hen, out of reach of her beak. It repeatedly attempted to peck at the eggs under the female's body, and when she refused to move it pecked and pulled at her tail feathers, often "holding her away" with one foot. The sitting hen chattered and clucked continually, and after five or six minutes the magpie flew off.

Probably the species creating the most disturbance for incubating peahens, however, is *Homo sapiens junior*. The open nature of Whipsnade means that the public have access to wide areas of the Park, and thus sitting females are occasionally flushed from the nest by inquisitive children. If such disturbance is rare, the hen returns to her clutch and continues incubation. However, if it occurs again within four days or so, particularly at the beginning of incubation, the female is likely to desert. The ease with which a female is flushed from the nest varies between individuals, but it appears both from observations of hens disturbed by children, and from my own nest monitoring, that hens become increasingly reluctant to leave the nest as incubation progresses. Older hens (such as the one described above) also

appear to be more tenacious than younger hens, but I have no empirical support for these conclusions.

3.6 Discussion and conclusions

The aim of this chapter was to investigate the nesting behaviour of peahens at Whipsnade, and to test the predictions of current reproductive effort theory regarding relative levels of parental investment. The hypotheses presented in Section 3.1.1 predict that peahens of any given age should expend more parental effort as their residual reproductive value declines, and as the reproductive value of their offspring increases (Williams 1966a,b; Trivers 1972; Hirshfield & Tinkle 1975; Curio 1988). Parental expenditure was investigated in both material and behavioural terms, and related to measures of clutch reproductive value and parental residual reproductive value.

Material investment

Seasonal trends

Egg size and number are positively correlated within the population, and therefore do not support the predictions of the simple trade-off model. Since both clutch size and egg size are likely to be related to parental quality and to the female's total parental expenditure, it is not surprising that both variables are positively linked. However, an individual female will have a certain defined level of investment which has to be divided among her clutch, and so there must still be a trade-off between size and number on an individual scale. For a given body size, egg size tends to be the least variable trait in many species, and clutch size is often the most variable (Western & Ssemakula 1982; Winkler & Wallin 1987). The range of both clutch size and egg size indicates that there is not a single optimum for the population, but that both are affected by individual levels of parental investment, and environmental conditions and resources. It is apparent however that peahen egg size varies much less than clutch size, and the range of optimal sizes is relatively small.

Egg size is often related to offspring survival (*e.g.* Parsons 1970, 1975; Grant 1991), and in many species egg size decreases and clutch size increases as environmental conditions

deteriorate (Bagenal 1969; Murton & Westwood 1977; Fraser 1980). One might thus expect eggs laid later in the breeding season to be larger, in order to increase the chance of chicks surviving over the winter (*e.g.* the great tit *Parus major*, Perrins 1970). However, at Whipsnade mean egg volume declines over the breeding season, in common with a number of other species (*e.g.* the herring gull *Larus argentatus* (Parsons 1975), the kittiwake *Rissa tridactyla* (Coulson 1963) and the gannet *Sula bassana* (Nelson 1966)). This decline might be explained by variation in constraints operating directly on egg size, if for example the resources available to hens for the manufacture of eggs decreases over the season. Figure 3.11 indicates that female body weight increases in early spring, but no morphological measurements were taken of hens over the breeding season. Measurements are needed of non-breeding hens, since the apparent decline in condition between April and October is almost certainly due to parental expenditure. It is unlikely that food availability for the female is responsible for the decline in egg volume, since it is increasing over the main part of the nesting season.

Nevertheless, the size of egg produced may still be related to environmental conditions affecting the chicks, if food availability for the chicks rather than overwinter survival is the most important factor. Peachicks feed predominantly on grass and weed seeds and insects, all of which increase in density from spring to late summer. The majority of chicks are hatched before these food supplies reach their peak, and larger egg size at the start of the season can therefore compensate for reduced food availability.

What are the advantages for peahens of nesting early in the season, before either nest cover or food supplies have reached their peak? Early breeding has been shown to improve chick survival in several species, for example the great tit *Parus major* (Perrins 1970; Perrins & McCleery 1989) and the Manx shearwater *Puffinus puffinus* (Perrins 1966), and early-hatched wood pigeon young *Columba palumbus* can complete their moult before winter (Murton *et al.* 1974). At Whipsnade, an obvious size discrepancy between chicks hatched early (*e.g.* June) and those hatched later (*e.g.* August) persists until winter, but unfortunately there are no data available on chick survival to breeding age.

Another advantage of nesting early is that it allows time for a second breeding attempt, should the first nest fail. Nest predation rates at Whipsnade are very high, and the effects of predation can be demonstrated by differences in nesting patterns between years. In 1990, the Zoo abandoned their usual policy of employing a gamekeeper to shoot crows, magpies and foxes. During that year I discovered many more predated egg shells than in the other two years, and the nesting season lasted for 100 days (1989 and 1991 were 63 and 75 days respectively). This indicates that hens were probably renesting after their first clutch was predated, but there was evidence of renesting only by females whose first clutches were laid before the end of June. It appears therefore that in peahens, the benefits of laying earlier outweigh the costs of sub-maximal nest cover and food availabilty.

The seasonal decline in clutch size observed at Whipsnade is common among bird species (Klomp 1970; Winkler & Walters 1983; Hamann & Cooke 1989). Various hypotheses have been proposed to account for this trend, the majority focussing on direct environmental effects rather than indirect life history effects. Explanations include smaller replacement clutches (*e.g.* Winkler & Walters 1983), reduced female reserves or nutrient availability (*e.g.* Ashmole 1963; Lack 1968; Ricklefs 1980; Hamann & Cooke 1989), changes in weather or vegetation (*e.g.* Royama 1966, 1969; Yom-Tov & Hilborn 1981), changes in population density and competition (*e.g.* Cody 1971), increased rates of nest parasitism or predation (*e.g.* Perrins 1977), trade-offs against an increase in egg size (*e.g.* Bagenal 1969; Murton & Westwood 1977; Fraser 1980), younger or poorer quality females nesting later (*e.g.* Mills 1973; Ryder 1980), and decreasing ability of hens to care for larger broods (*e.g.* Lack 1968; Winkler & Walters 1983).

Winkler & Walters (1983) believe that much of the variation in clutch size is due to smaller replacement clutches, but that seasonal trends persist when the effects of replacement clutches are removed. The secondary clutches of very few marked peahens were discovered during the study, but of these there was no consistent decrease in clutch size. This hypothesis cannot therefore be discarded, since there are insufficient data. Even if further observations discover that peahens do lay fewer eggs the second time around, we still need

to disentangle which evolutionary and selection pressures are responsible for the decline, and whether these factors similarly affect hens laying their first clutches late.

It is unlikely that the reserves of females are declining over the season, for the reasons given with respect to egg size, above. Similarly, vegetation and nest cover is increasing in density throughout the main part of the nesting season, as clutch size is decreasing. Peahens in India time their breeding to coincide with the peak of insect density, which is during the monsoon, but in England the warmer weather increases the number of insects and seeds available. Another possible explanation is that clutch size is limited by the availability of water, and clutch size decreases over time with rainfall; however, water supplies are always available at Whipsnade, and do not appear to be a constraining factor. Variations in temperature and sunshine are also unlikely to affect clutch size directly (*e.g.* by changing constraints of egg reheating or cooling), as nests are generally protected against direct sun by vegetation; and since larger clutches require more reheating (Smith 1989), one would rather expect larger clutches to occur later in the season.

The huge area of Whipsnade Park means that competition, either for nest sites or chick food, is minimal, and is not likely to affect clutch sizes. Hens may lay smaller clutches as a defence against predation or nest parasitism. Larger clutches take longer to lay, and are therefore exposed to both dangers for a longer period; thus if predation or INP increases over the season, clutch size may decrease. However, Perrins (1977) demonstrated that unrealistically high clutch sizes and predation rates are necessary for predation to limit clutch size in this manner in precocial birds, and would result in only 5% of nests being successful for most galliforms. Slagsvold (1982, 1984) and Milonoff (1989) showed that predation rates can determine clutch size, if females are limiting the number of eggs they lay at their first attempt in order to save some reserves for renesting. Milonoff (1989) also argued that it may be profitable to allocate more reserves to the second clutch, even at the risk of the female's own survival or later reproduction, otherwise she has wasted a whole reproductive season. If predation affects clutch size in this way, one might expect an increase in size between attempts, in contrast to the observed trend. With regard to nest parasitism, my

study has also shown that INP is most common early in the breeding season, and should not therefore generate the observed seasonal decline in clutch size.

Decreasing clutch size does not result from a trade-off against increasing egg size, since egg size also decreases over the season. From the limited data available, it appears that young hens are laying significantly earlier in the season than older ones, and are laying slightly larger clutches, which contradicts the predictions of the hypothesis above. If older females are laying smaller clutches, this does not seem to support the theories of reproductive effort, which predict that hens should increase their parental expenditure as their residual reproductive value declines. However, it is possible that older hens may be delaying reproduction in order to parasitise the nests of conspecifics (Section 3.4.2), and the increase in chick production gained by this strategy may allow (or constrain) them to lay fewer eggs in their own nests. Further empirical evidence is required to support this hypothesis.

Heavy hens tend to nest earlier than light ones (Figure 3.12), and declining clutch size may be the result of smaller females taking longer to build up the energy reserves necessary for breeding, and then laying smaller clutches (see below). The size and condition of females needs to be measured at the time of nesting though, for this hypothesis to be tested.

Lack (1954, 1968) hypothesised that the clutch sizes of birds have been adapted by natural selection to correspond with the largest number of young for which the parents can, on average, provide sufficient food or care. In precocial species which feed their young little or not at all, the costs of parental care have in the past been widely assumed to be negligible (*e.g.* Kendeigh 1952). Certainly, the energy demands of precocial chicks are considerably lower than those of altricial chicks, but nevertheless it is now recognised that the time and energy costs of caring for nidifugous young can be considerable (*e.g.* Winkler & Walters 1983). The costs of brooding in peafowl, in terms of both time and brood defense, are investigated in Chapters Four and Five. If the ability to care for chicks is responsible for the observed decline in clutch size, the costs of caring must (a) increase over the season, and (b) be correlated with brood size. The relationship between parental expenditure and brood size will be discussed further in the following two Chapters; but in any case the costs of caring

for a brood are likely to decrease over the season, for many of the reasons outlined above (*e.g.* increasing food supplies for the chicks).

Many of the explanations of a seasonal decline in clutch size are not applicable to the population at Whipsnade. The three most convincing hypotheses appear to be that replacement clutches are smaller than initial nesting attempts, lighter hens nest later than heavy hens and lay smaller clutches, and that nest parasitism by older females constrains or allows them to lay fewer eggs in their own nests later on. Further observations (and possibly brood manipulation experiments) are needed to test these conclusions empirically.

Reproductive value theory

The fitness costs of reproduction to young animals may be higher than to old animals (Clutton-Brock 1991; see also Chapter One), because (i) studies suggest that the energetic costs of breeding and their influence on survival may be greater in young or novice breeders; (ii) in animals that continue to grow after reaching breeding age, reproduction may delay or prevent the attainment of maximum size; and (iii) where survival declines with age, a given risk of dying as a result of breeding represents a larger cost to younger animals (Williams 1966b; Pianka 1976; Curio 1988).

Reproductive value theory thus predicts that older females, with lower residual reproductive value, should invest more than younger females, by laying larger eggs and larger clutches earlier in the season (Williams 1966b; Curio 1988). Reproductive success is lower for young individuals in many species, but it has not been demonstrated that this results from lower expenditure by young females rather than from lack of skill (Lack 1966; Curio 1983; Clutton-Brock 1991). The data presented in Figure 3.10 do not support this hypothesis: mean egg size is almost identical for the two categories, clutch size is slightly negatively correlated with age, and young hens lay significantly earlier in the season than older hens.

In contrast, the hypotheses regarding levels of expenditure in relation to body size and condition are not rejected: although none of the relationships are significant, heavier females tend to produce larger clutches and larger eggs, and lay earlier in the season. The explanation may be that smaller hens have lower fat reserves and smaller oviducts, which

can lead to fewer, smaller eggs, and smaller hens need a longer period to build up their energy reserves before initiating laying.

Evidence in support of reproductive value theory would be that hens invest more in subsequent breeding seasons, as their residual reproductive value declines. There was however no significant increase in either clutch size or egg volume for the few individual females recorded, either within or between years (Figure 3.13).

An alternative explanation for the difference in clutch size between old and young hens involves the strategy of INP (see above). Before these theories can be untangled, more data are needed on exact female age and condition at the time of breeding, and the relationship between them; also on which hens are responsible for nest parasitism. It appears therefore that the level of material investment in clutches may be a result of physiological constraints, such as body size or condition, rather than a response to residual reproductive value.

Behavioural investment

Reproductive value theory predicts that parental behaviour displayed by incubating hens should be related to the reproductive value of the clutch. One would therefore expect vigilance, nest attendance and egg rolling to be positively correlated with clutch size, egg volume and stage of incubation, and negatively with date of lay. However, it is important to remember that female quality may affect both material and behavioural measures of expenditure independently, and not to infer too much from any apparent relationship between the two measures.

The levels of vigilance displayed by incubating hens are positively correlated with all four measures of clutch reproductive value, and would thus seem to support the reproductive value theory. However, peahens may be adjusting their levels of expenditure in relation not only to the reproductive value of their offspring, but to additional factors which are in turn related to clutch variables (*e.g.* female quality; see above). The main difficulty of finding out what determines vigilance is to ascertain what the animals are being vigilant for (see Lazarus 1990). For example, if the aim of the behaviour pattern is to detect predators, the risk of predation may be independent of clutch size, egg size and stage of incubation, but be

positively or negatively correlated with laying date; whereas if the purpose of vigilance is to detect nest parasites, the clutch is most at risk early in the season and early in incubation. Large clutches are also more at risk of INP than small, and these factors could confound the effects of offspring reproductive value on levels of vigilance.

From stepwise regression analysis, it appears that clutch size is the most important variable determining the level of vigilance. Although vigilance can be described as an "unshared" component of parental expenditure (Lazarus & Inglis 1978, 1986), and so might not be expected to increase with clutch size, larger clutches are still of a higher value and parents should expend relatively more on them (Lazarus & Inglis 1978; Barash 1982). Brood predators of precocial species such as peafowl are also more likely to take single chicks than the whole brood, and so vigilance would thus be expected to increase with brood size (Lazarus & Inglis 1986). If hens are investing according to clutch reproductive value, then an increase in clutch size would appear to be worth more (*i.e.* potentially fledge more young) than increased egg volume or earlier laying. This begs the question of why females do not lay larger clutches; galliformes have been shown to be indeterminate layers (*e.g.* Lack 1947, 1954, 1968), capable of laying many more eggs than the average clutch size. Before this question can be addressed fully, the constraints limiting clutch size need to be determined, for example through brood manipulation experiments.

There is no significant relationship between nest attendance and clutch size, egg size or incubation stage. However, there appears to be a trend for peahens to show increased nest attendance for larger clutches, larger eggs and older eggs, which is again in the direction predicted by reproductive value theory; but it is also possible that, for example, the costs of reheating larger eggs and clutches are greater than smaller ones, or larger clutches may be more vulnerable to predation, and hens therefore spend less time away from the nest in order to minimise this effect. The best predictor of nest attendance is incubation stage, and this provides more convincing evidence that females may be adjusting expenditure on attendance in relation to clutch reproductive value.

Time spent turning eggs is not significantly related to any clutch parameter. Nevertheless, there is a slight tendency for larger clutches, later in the season, to be turned more.

However, although the relationship between egg turning and incubation stage is almost significant, it is not in the direction predicted by reproductive value theory. It is possible that the physiological requirements of developing embryos mean that earlier ones need more turning than later ones; for example, Deeming (1991) reports that the critical period for turning in domestic fowl is days 3-7, since turning prevents adhesion and stimulates the growth of blood vessels. However, some of the literature suggests the opposite is true (Skutch 1976; Welty & Baptista 1988). The causal or functional explanation of this finding thus remains a mystery.

The theory described above, that older hens should invest more in clutches than young ones, relates also to behavioural expenditure. Thus old hens would be expected to be more vigilant, more attentive, and roll eggs more than young hens. Figure 3.19 shows that female age is significantly related to only one behaviour pattern, vigilance, but the relationship is in the opposite direction from that predicted. Similarly, although there is no significant relationship between female age and either nest attendance or egg turning, there is a slight tendency for younger females to be more attentive than older ones; thus the parental residual reproductive value hypothesis again appears to be refuted.

With regard to female weight, there is a significant positive relationship with vigilance, but no significant correlation with either nest attendance or egg turning. In common with material investment, the data for vigilance support the predictions of the constraint hypothesis, that heavier hens invest more in vigilance than lighter ones; and even the other two behaviour patterns, although not significant, may indicate a tendency for heavier hens to be more attentive and to turn eggs more frequently. The support of the constraint hypothesis is perhaps more easily explicable in the context of material than behavioural investment. However, larger hens are likely to have more reserves to allocate to nesting, and so may not need to be absent from the nest to feed for as long as small hens; but the basis for the relationship between body size, vigilance and egg turning is less clear.

Conclusions

Levels of behavioural investment in nesting generally support the hypothesis that hens invest more in clutches of higher reproductive value. However, firm conclusions cannot be drawn until the effects of confounding variables, such as differences in female quality, predation risk and the function of vigilance, are removed.

The predictions of reproductive value theory regarding investment in relation to parental residual reproductive value (*i.e.* that older hens should invest more than younger ones) are not supported; in fact the few significant relationships appear to be in the opposite direction to that predicted. It would therefore be reasonable to conclude that the assumptions upon which the theory is based may not be applicable to hens at Whipsnade. Peahens do not continue to grow once they have reached breeding age, and there is some evidence that young females may be in better condition than old ones, so that the energetic costs of reproduction increase with age. It has also not been shown that survival decreases with age; it may be that once a peahen reaches maturity, her expectation of mortality remains fairly constant until approaching the end of her expected lifespan, when terminal investment would be expected to increase. Nevertheless, even a constant mortality risk should mean that young hens have more to lose by dying as a result of breeding than old hens, and so would be expected to invest relatively less.

Nest parasitism and dump nesting have been discussed fully in Section 3.4, and it appears that the two strategies may be related. Both single eggs and large dump nests may be the result of physiological or environmental constraints, and dump nests may be a misguided attempt at INP. The large volume of dumped eggs is unexplained. Intra-clutch variation in eggs is lower than inter-clutch variation, but this does not appear to result in the rejection of foreign eggs. Possible adaptive explanations for the acceptance of alien eggs assume that the costs of rejection are higher than the costs of acceptance, perhaps because the risk of ejecting a host egg is greater than the cost of caring for a larger clutch (and brood).

It is suggested that old hens may be parasitising the nests of young ones, before laying their own clutch. The hatching success of parasitic eggs is considerably lower than either host

eggs or non-parasitised clutches, but if INP exists as part of a mixed strategy, overall chick production may be enhanced.

In summary, I conclude that investment in nesting is generally related to the reproductive value of the offspring, but that constraints of body size and condition may be better predictors of expenditure than the residual reproductive value of the female. Nest parasitism is an adaptive strategy if older hens are parasitising the clutches of younger hens before laying their own clutch, thereby increasing their own overall reproductive success.

CHAPTER FOUR

PARENTAL INVESTMENT IN BROODING: BROOD DEFENCE

4.1 Introduction

The predominant cause of chick mortality in most species of birds is predation (Ricklefs 1969; Cody 1971). Predation is therefore a powerful selective pressure, and any measure that parents take to enhance offspring survival can increase their inclusive fitness. Brood defence has often been shown to improve the chances of young surviving to reproduce (*e.g.* Grieg-Smith 1980; Brunton 1990; Wiklund 1990a,b), but at some assumed risk to the parent itself (*e.g.* Barash 1975; Grieg-Smith 1980; Blancher & Robertson 1982; Walters 1982; Brunton 1986). If a parent sacrifices its own life to protect its brood, not only has the parent forfeited the opportunity to breed again, but the current brood may also perish without parental care. Parental investment theory predicts that selection should result in a level of defence that is a compromise between the fitness gain to the current brood, and the gain to future broods from parental survival (Williams 1966a,b; Trivers 1972; Lazarus & Inglis 1986; Curio 1988).

Hypotheses regarding relative levels of parental expenditure on defence are scattered throughout the literature, but many of the predictions are difficult to test experimentally. The benefit of defence to the offspring is presumably increased survival, but to measure this effect we would need to determine how levels of defence affect the probability of survival, as well as the probability of survival with and without a defending parent; yet this does not take into account that the mere presence of an adult may be sufficient to deter many a predator from attacking a brood, even in the absence of active defence. The costs to the parent are equally complicated and indefinable, since they incorporate not only the time and energy costs of vigilance and brood defence, but also the costs in terms of risk of injury or death (*cf.* Lazarus & Inglis 1978; Grieg-Smith 1980). Nevertheless, predictions can be made about brood defence by means of comparative studies.

The observed level of parental defence may be related to various components of reproductive value, or may be a non-adaptive result of physiological or environmental constraints, but is likely to be a compromise between both. Discussed below are factors that may influence the degree of defence shown by different individuals.

- *Offspring age.* Reproductive effort theory predicts that the reproductive value of offspring will increase with age, for the following reasons: (i) there is less potential for adults to renest as time goes on (Barash 1975; see "Time in season", below); (ii) the expected benefits of parental investment increase, while the expected costs decrease (Dawkins & Carlisle 1976; Boucher 1977); and (iii) the difference between adult and juvenile survival probabilities diminishes (Andersson *et al.* 1980; Montgomerie & Weatherhead 1988). If parents invest in brood defence according to offspring reproductive value, then one would expect defence to increase with offspring age (Williams 1966b; Trivers 1972).

- *Offspring quality.* If higher quality juveniles have a higher probability of survival, then parents might be expected to invest more in them in terms of defence (Boucher 1977; O'Connor 1978; Carlisle 1985; Montgomerie & Weatherhead 1988).

- *Brood size.* Brood defence is defined as an "unshared" component of parental investment (Lazarus & Inglis 1986), since the benefits are gained simultaneously by all members of the brood, and is thus expected to be independent of brood size (Section 1.3.3). Similarly, the risks to the parent of defending its brood should vary independently of the number of chicks being defended (Montgomerie & Weatherhead 1988). However, the relationship between brood size and defence will depend upon the type of predator typically encountered. If predators generally take an entire brood, then the level of defence shown by the parent should increase with brood size, since the size of a brood is assumed to be proportional to its reproductive value (or some equivalent cohortal measure, as favoured by Onnebrink & Curio 1991), and the benefits of deterring a predator will consequently increase with offspring number (Lazarus & Inglis 1986; Montgomerie & Weatherhead 1988). In contrast, if predators usually take only

one member of a brood at a time, the benefits of defence will be constant, and we would predict that defence should be irrespective of brood size (Lazarus & Inglis 1978, 1986).

- *Parental age.* In species with age-dependent senescence, reproductive value theory predicts that parental effort increases as parental residual reproductive value declines (Williams 1966b). Thus older parents should exhibit greater brood defence than younger ones. However, care must be taken to account for the effects of parental experience, which is likely to increase with parental age (*e.g.* Thornhill 1989).

- *Parental quality.* The quality or condition of a parent may constrain the amount of time or energetic reserves available for defence, and hence better quality individuals may defend broods more vigorously than poor quality parents.

- *Time in breeding season.* As the breeding season progresses, the opportunities available for renesting decline, and the current reproductive attempt therefore becomes increasingly valuable (Curio *et al.* 1984; Redondo *et al.* 1989). On this basis, parents are expected to defend later broods more than earlier ones, all other things being equal. However, later broods often have a lower chance of survival and are therefore of lower value, and the parent may invest less in later broods (Onnebrink & Curio 1991).

- *Observer disturbance.* Many authors have reported an increase in brood defence over a season (*e.g.* Barash 1975; Grieg-Smith 1980; Brunton 1990), and have attributed it, for example, to offspring age, vulnerability or renesting potential. However, Knight & Temple (1986) suggested that this observation is largely a result of the methods used by researchers, since repeated visits to a nest can result in modification of defence behaviour by positive reinforcement and loss of fear, and few studies have controlled for revisitation (*e.g.* Regelmann & Curio 1983). Westmoreland (1989) found that although there was no significant difference in response between single and repeated visits, there was an increased chance of finding significant differences between individuals (*i.e.* committing a Type I error) with multiple visit analysis.

- *Vulnerability of offspring.* According to the "vulnerability hypothesis", parents should exhibit a greater level of defence of more vulnerable offspring. In altricial birds, chicks

become increasingly vulnerable as their bodily demands and their development render them ever more conspicuous, thus attracting the attention of predators and/or cannibals (Harvey & Greenwood 1978; Onnebrink & Curio 1991). Brood defence is therefore predicted to intensify from hatching to fledging, and such an increase has been observed in many species, as described above. However, the majority of studies have concentrated on altricial species, and observed increases in the intensity of nest defence have widely been attributed to offspring age and resulting changes in value.

The selection pressures on defence in altricial and precocial species are very different (Barash 1975). In precocial birds, chicks become less vulnerable with age; thus brood defence is predicted to peak at hatching, and subsequently decrease until fledging (Simmons 1955; Armstrong 1956; Montgomerie & Weatherhead 1988; Brunton 1990). Brunton (1990) modelled two hypotheses, one predicting that brood defence is correlated with offspring age, and the other that defence depends on chick vulnerability (see also Montgomerie & Weatherhead 1988). Different models were proposed for altricial and precocial species (Figure 4.1). She then tested the response of a precocial species, the killdeer *Charadrius vociferous*, and found that defence increased during the nesting period (in accordance with the "age" hypothesis), but declined after hatching (thus supporting the "vulnerability" hypothesis).

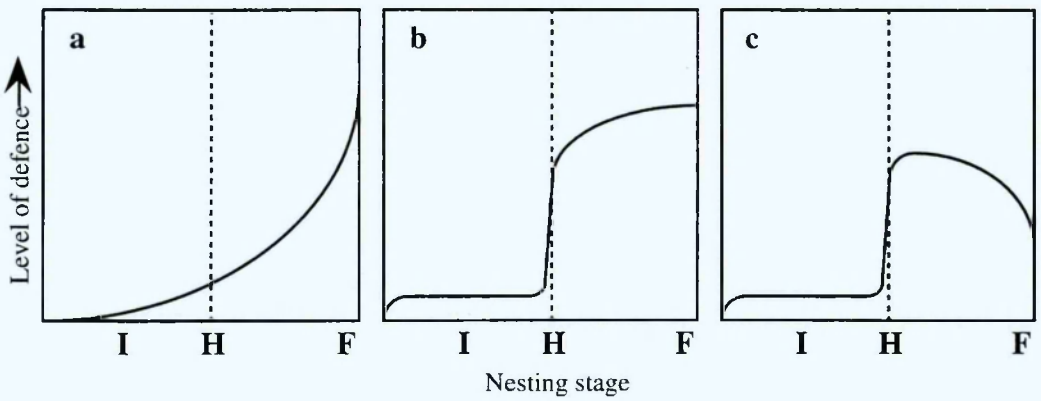


Figure 4.1. Graphical representation of models of parental defence (adapted from Brunton 1990). Stages of nesting: I = incubation; H = hatching; F = fledging. (a) Model 1 predicts that levels of parental defence correlate with offspring age. Model 2 predicts that levels of parental defence correlate with offspring vulnerability, which (b) in altricial species continues to increase after hatching, and (c) in precocial species declines after hatching.

It is apparent that the theories described above give rise to a minefield of conflicting and confounding predictions, and it is perhaps not surprising that most studies have selected only certain elements of the hypotheses to test. For example, an observed increase in nest defence over a season may be due to offspring age, vulnerability or renesting potential; greater intensity of defence of larger broods may be because they are of a higher reproductive value, or because higher quality parents produce larger broods and also invest more in defence.

Some confounding factors can be removed or controlled for by brood manipulation experiments. Carlisle (1985) examined brood defence in a cichlid fish *Aequidens coeruleopunctatus*, and, by experimentally augmenting or reducing brood sizes, showed that females invest according to current brood size, regardless of parental quality, previous investment, or experience. Thornhill (1989) similarly investigated nest defence in red junglefowl *Gallus gallus spadiceus*, a species displaying age-dependent senescence. By using hens of known age and breeding experience, and by exchanging clutches and broods of different sizes and ages, he demonstrated that females appear to invest according to reproductive effort theory. Both old and young females showed greater defence of the second nest than the first within a season; old hens were more defensive than young ones; all females defended chicks more than eggs; and larger broods were defended more than smaller.

Experimental manipulations such as the studies of Carlisle (1985) and Thornhill (1989) can elegantly discriminate between brood defence hypotheses, but tests of predictions in the field are considerably more difficult. Observations should be based upon comparisons between broods of different sizes and ages, and parents of known age and condition, at different times in the breeding season. However, some of these variables (*e.g.* parental condition) may not be measurable at the time of observation. In addition, brood size often declines through the breeding season due to natural predation or mortality rates (perhaps affecting precocial species more than altricial), so defence measurements of large broods at the end of the season may incidentally be biased towards parents of higher quality, which have produced larger broods or shown superior defence up to that point.

4.2 Brood defence at Whipsnade

4.2.1 Peahens as precocial parents

Altricial and precocial species differ not only in the mode of chick development, but also with regard to the variety of behaviour displayed in defence of those chicks. In altricial species, defensive behaviour commonly takes the form of one or both parents giving alarm calls and mobbing or threatening a predator; models of nest defence have thus generally been tested by recording the relative intensity of these behaviour patterns, and occasionally the proximity of a mock predator or the researcher to the nest before flushing. The defence of a nidifugous brood is likely to differ from the defence of young localised in a nest, but few quantitative studies have been conducted on precocial species.

Brood defence in precocial birds often includes a spread-wing distraction display, during which adults characteristically feign injury and attempt to draw a predator away from their offspring (Simmons 1955; Pedersen & Steen 1985; Brunton 1990; Hudson & Newborn 1990). This strategy may be successful in fooling some predators, but in other cases the display may be used as a stimulus to search for the nearby brood (Sonerud 1988; Hudson & Newborn 1990). An alternative option for a parent with a nidifugous brood is simply to lead the chicks away from the predator. Assuming that a predator can move faster than a brood of chicks, a parent has the choice of approaching and attacking the predator (high risk), staying with the brood as a deterrent (medium risk), or abandoning the chicks and fleeing (low risk); I suggest that each of these strategies represents a point along a continuum of costs for the parent and benefit for the current brood (Figure 4.2; see also Montgomerie & Weatherhead 1988). Optimality theory predicts that the greatest net fitness gain occurs at the point (*) where the difference between cost and benefit curves is maximised.

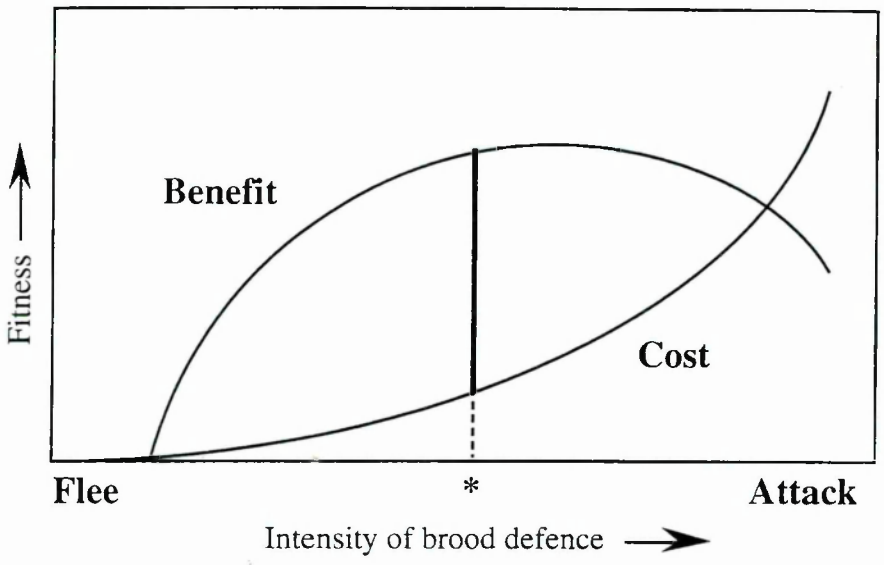


Figure 4.2. Graphical model of defence of a precocial brood. Fitness benefits are determined by survival of the current brood; fitness costs are the loss of future reproductive success as a result of injury or death of the parent. The optimal intensity of brood defence occurs at the point (*) of maximum difference between benefits and costs. (Adapted from Montgomerie & Weatherhead's (1988) model of nest defence in altricial species; see also Trivers 1974.)

Peahens have never been reported to give distraction displays in the presence of a predator. Brood defence should depend upon whether the predator is a threat to the female as well as the chicks; at Whipsnade, the main predators of chicks are corvids, mustelids, storks and foxes, and human disturbance is also frequently responsible for brood dispersal. Crows, magpies, stoats and weasels may not be a serious threat to an adult peahen, but only one direct attack by these predators was seen. I did however observe several fatal attacks on chicks by white storks *Ciconia ciconia* (Plate 4.1). Only once was a peahen seen to retaliate against the larger, more aggressive stork (Plate 4.2), and on this occasion brood defence was unsuccessful, with the peahen losing one of her chicks to the attacker. From the evidence of peafowl carcasses, foxes *Vulpes vulpes* were also known to be predators of adults as well as their broods.

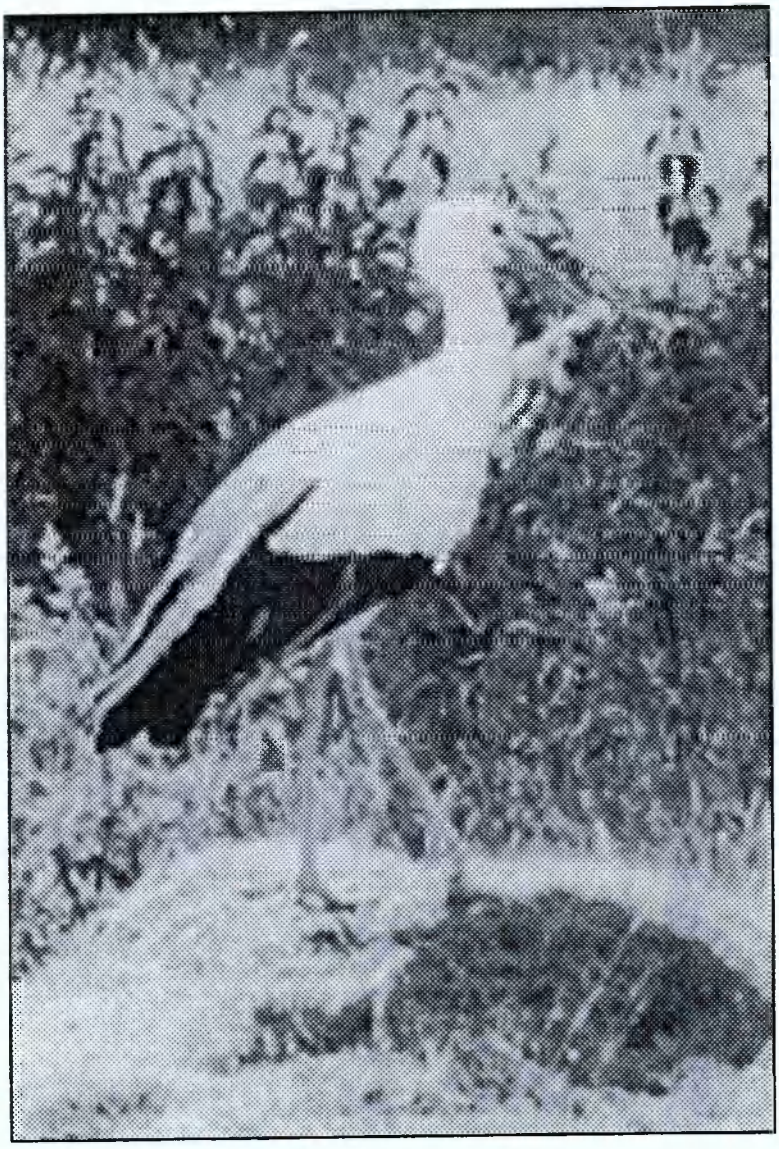


Plate 4.1. Fatal attack on a peachick by a white stork *Ciconia ciconia*. Additional evidence for such attacks was provided by the presence of metal patagial tags in stork faeces.

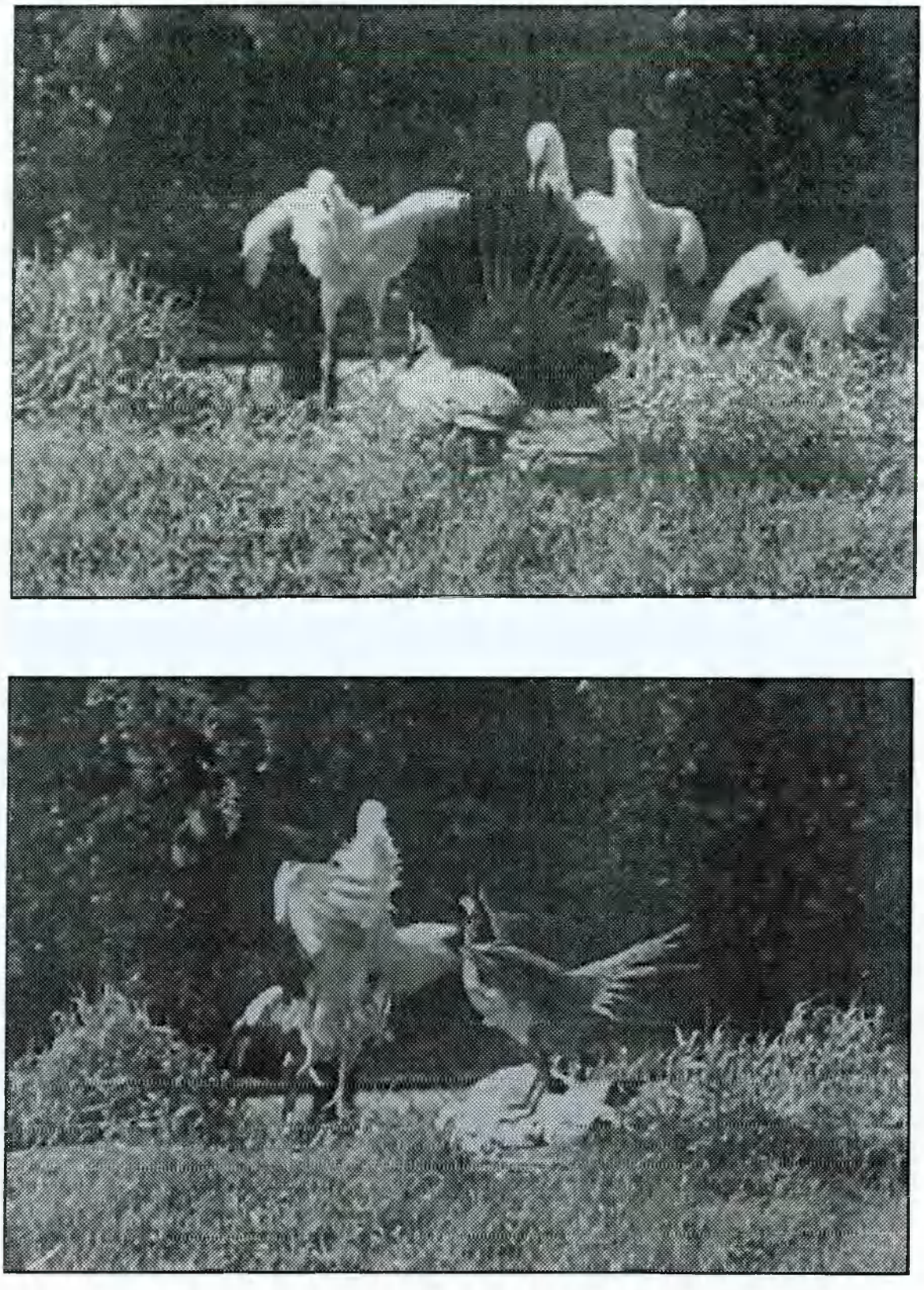


Plate 4.2. Attempted brood defence by a peahen against attack by a white stork *Ciconia ciconia*. *a:* Hen displaying to stork; *b:* Aerial combat (the peahen lost).

Adult peafowl at Whipsnade also have reason to be wary of humans, as a result of both the large numbers of visitors and the long-term trapping programme there, and humans may therefore be regarded as the equivalent of a natural predator. When approached by a human, non-parent birds immediately flee, usually in silence, although territorial males tend to be less cautious during the breeding season (indulging in what Sharma (1978) terms "erotomania negligence"!). Parent females, however, exhibit a range of behaviour when approached by humans, from fleeing at once to remaining with the chicks and displaying to the intruder. A defensive or aggressive display by a peahen normally consists only of raising her tail and lowering her wings (Plates 4.2*a*, 4.3), in a manner similar to the male's threat display, but on one occasion I was physically attacked by a peahen while collecting her two young chicks for marking.

Plate 4.3. Defensive display by a broody peahen, showing raised tail, lowered wings and erect nect feathers (hen's chicks are out of picture).

4.2.2 Methods

I argue that a peahen's response to a human may be used as a valid measure of her investment in brood defence, since a female remaining with her brood when approached by a human is doing so at some perceived risk to herself. Consequently I have used a simple

measure of defence, namely the minimum distance a parent allows a human to approach before fleeing. I approached each subject on foot, at a steady walking pace, moving directly towards the hen. Records were made of the initial distance before starting to approach the hen, and of the minimum distance that each female permitted me to get to her and her brood, before running or flying away; this latter measure is hereafter termed "predator distance".

Peahens with broods in three age categories were tested. The first category consisted of chicks with egg teeth, which were up to approximately two days old (Plate 4.4); the second included chicks of 7-10 days old (as judged from size, development and knowledge of hatching dates), and the third category consisted of chicks close to fledging, at around three weeks old (Plate 4.5). One of the aims of this project was to capture all chicks for marking and taking blood (see Chapter Five). In order that previous experience with marking did not affect either a peahen's or her brood's response to me, predator distance was recorded prior to any attempt at capture. There were sufficient uncaptured broods in each category for testing.

Plate 4.4. Newly hatched peachick, still with egg tooth and feathers in shafts.

Plate 4.5. Peachick approximately three weeks old.

Hatching dates ranged from early June to early September, and so defence could be tested at various stages in the season. Although peahens at Whipsnade were accustomed to human disturbance, I wished to avoid the potential problems of repeated visits to the same individuals (Knight & Temple 1986), and of statistical Type I errors from analysis of multiple visits (Westmoreland 1989); I therefore recorded predator distance from each hen only once in a season, although the same female might be used in different years. "Time in season" was divided into three categories, according to when the brood was known or estimated to have hatched: before July 15th, July 15th to August 14th, and August 15th onwards.

Additional records included whether the hen was alone or in a group at the start of the approach, the existence of any aggressive tail-up display; and any alarm calls by the female. Predator distances were compared for females with broods of various sizes and ages, at different times of the season. A few data were also available on female ages and relative weights, but these could not be obtained from hens at the time of breeding and were extrapolated from winter capture records (see Section 3.2). "Young" hens were known to

be two, three or four years old at the time of breeding; "old" females were known to be at least five years old. The threshold between "light" and "heavy" females was the median value (3.345kg) at the time of the last measured adult weight.

4.2.3 Hypotheses and predictions

The data obtained were used to test the following hypotheses, which relate to various measures of offspring and parental residual reproductive value, and environmental constraints, as discussed above.

Experimental validity

Hypothesis H_1 "Predator distance", as defined above, is a valid measurement of investment.

Prediction: Females with broods will allow me to approach closer than non-parent hens.

Hypothesis H_0 The measure used is not valid.

Prediction: There will be no significant difference between the responses of hens with and without broods.

Chick age

Hypothesis H_1 Peahens invest in a brood according to its reproductive value.

Prediction: Females will be more defensive of older chicks.

Hypothesis H_2 Peahens invest in a brood according to chick vulnerability.

Prediction: Females will be more defensive of younger chicks.

Hypothesis H_0 Neither chick reproductive value or vulnerability individually influence investment in brood defence.

Prediction: Intensity of defence will not be significantly related to chick age.

Brood size

Hypothesis H_1 Peahens invest in a brood according to its reproductive value; alternatively, hens invest according to the "brood loss" case of unshared parental expenditure (*i.e.* predators typically take entire broods at a time).

Prediction: Females will be more defensive of larger broods.

Hypothesis H_2 Peahens invest in broods according to the "fixed loss" case of unshared parental expenditure (*i.e.* predators typically take single chicks).

Prediction: Intensity of defence will not be significantly related to brood size.

Time in season

Hypothesis H_1 Peahens invest in their broods according to their reproductive value.

Prediction: Females will be more defensive of earlier broods, which have a higher probability of survival.

Hypothesis H_2 Peahens invest in their broods according to renesting potential.

Prediction: Females will be more defensive of later broods, since the opportunities available for renesting decline as the season progresses.

Hypothesis H_0 Investment in brood defence is not individually related to either offspring reproductive value or renesting potential.

Prediction: Intensity of defence will not be significantly related to time in season.

Female age

Hypothesis H_1 Peahens invest in defence according to their own residual reproductive value.

Prediction: Older females will be more defensive than younger ones.

Hypothesis H_0 Investment in defence is not determined by female residual reproductive value.

Prediction: Intensity of defence will not be significantly related to female age.

Female weight

Hypothesis H_1 Investment in defence is constrained by female body condition.

Prediction: Heavier hens will be more defensive than lighter ones.

Hypothesis H_0 Investment in defence is unrelated to body condition.

Prediction: Intensity of defence will not be significantly related to female weight.

4.3 Results

4.3.1 Experiments and observations

Experimental validity

The measure of "predator distance" appears to be a valid measurement of parental investment in brood defence. Females with broods up to fledging age allowed me to approach

significantly closer than non-parent birds (Figure 4.3), and all displayed raised tails and lowered wings on my approach. Whether the focal peahen was alone or in a group had no effect on predator distance, since females generally saw me from the start of my approach. There were no consistent differences between hens in the rate of alarm calling; nearly all females gave loud alarm "honks" as I approached their brood. No non-parent hens gave either alarm calls or "tail-up" displays.

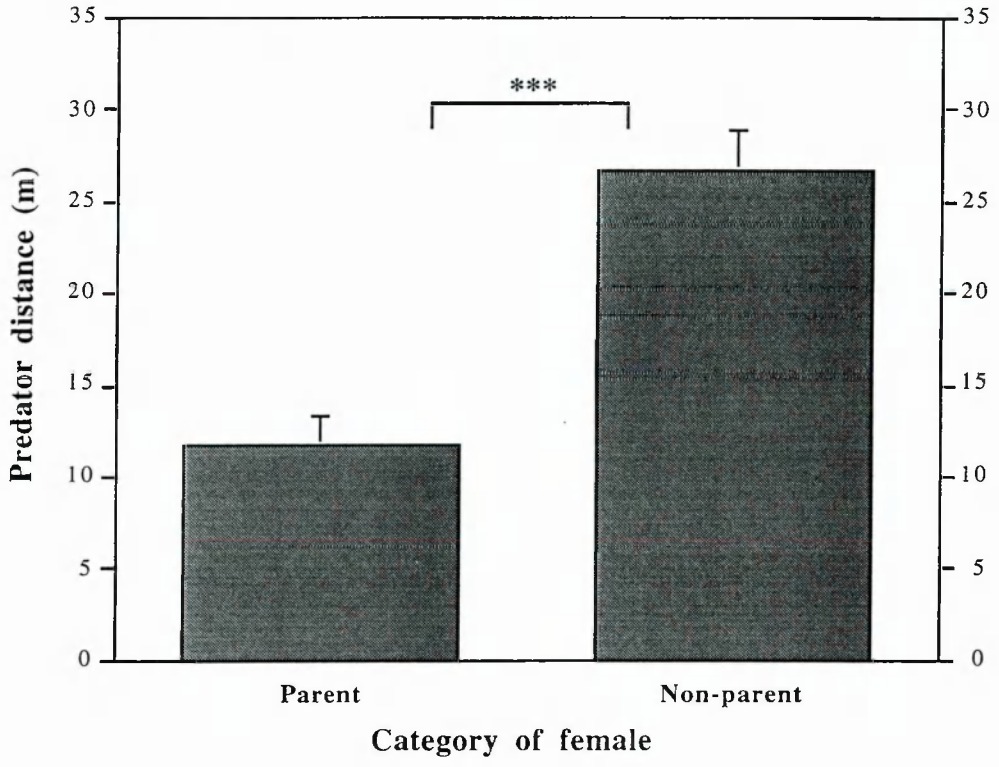


Figure 4.3. "Predator distances" of females with broods and non-parent hens. Error bars represent one standard error of the mean. Data were compared using a Mann-Whitney U test, corrected for ties ($n_1 = 40$, $n_2 = 27$, $U' = 927.5$, $p < 0.00003$).

Observations

Table 4.1 gives non-parametric tests of the relationships between each of the five variables and predator distance. The table shows that female weight, brood age and brood size are each significantly related to predator distance. However, these tests do not account for any relationships between the measured variables. Table 4.2 shows the interaction of the five variables with one another, using chi-squared and contingency table analysis. The interactions of brood size with each variable have also been analysed using Spearman's rank correlation coefficients. The Spearman test is more practical than using contingency table

analysis, since the data would have to be divided into seven brood size categories, each with a very small n, leaving little opportunity for significant results. The results of both analyses are shown in Table 4.2.

	Female age	Female weight	Brood age	Brood size	Time in season
Total N	31 (n_1 = 9, n_2 = 22)	31 (n_1 = 15, n_2 = 16)	40	40	40
Statistical test	Mann-Whitney U test	Mann-Whitney U test	Spearman's rank correl. coeff.	Spearman's rank correl. coeff.	Spearman's rank correl. coeff.
Statistic	U' = 103	U' = 172	ρ = 0.833	ρ = -0.511	ρ = 0.029
Significance	p = 0.4325	p = 0.0197	p < 0.00003	p = 0.0007	p = 0.4286

Table 4.1. Relationships between each of five variables and "predator distance". Data are analysed using Mann-Whitney U tests (for variables with two categories) and Spearman's rank correlation coefficients, corrected for ties (for variables with three or more categories). The resulting statistics and their associated significance levels are also given.

Variable (No. categories)		**Female age** (2)	**Female weight** (2)	**Brood age** (3)	**Time in season** (3)
Female weight (2)	χ^2 p	0.079 0.7787			
Brood age (3)	χ^2 p	3.217 0.2002	0.279 0.8699		
Time in season (3)	χ^2 p	3.751 0.1533	12.009 **0.0025**	2.418 0.6593	
Brood size (7)	χ^2 p	1.902 0.9285	1.178 0.9779	5.959 0.9181	10.021 0.6141
Brood size (correlation)	ρ p	– 0.020 0.4562	0.102 0.2877	– 0.298 **0.0314**	– 0.358 **0.0125**

Table 4.2. Interaction among each of five variables. The degree of interaction is determined by chi-squared and contingency table analyses. The large number of categories of brood size means that there is little chance of detecting interactions using a chi-squared test; hence these relationships are additionally analysed using Spearman's rank correlation coefficients. Significance levels for each interaction are also given, and significant interactions are highlighted in bold.

Table 4.2 shows that there are three significant interactions between the variables. Female weight is significantly related to time in season; *i.e.* heavy hens raise broods earlier in the season than lighter hens. Brood size is negatively correlated significantly with both brood age (predominantly due to natural chick mortality between hatching and fledging) and time in season (large broods occur earlier in the season than small broods; this agrees with the

findings of Chapter Three, that larger clutches occur earlier). Given that not all of the variables are independent, stepwise regression analysis is desirable in order to determine which of the variables most influence the intensity of brood defence observed (Table 4.3). The regression model of best fit (*i.e.* the model with the lowest p value) is given in Table 4.4.

Variable:	**Female age**	**Female weight**	**Brood age**	**Brood size**	**Time in season**	**Intercept**	**Signif-icance**
Coefficient	0.6943	– 5.0814	7.4192	– 1.8567	– 2.1540	14.1380	
p =	*0.7548*	*0.0137*	*1 x 10^{-7}*	*0.0010*	*0.0793*	*0.0227*	*1.78 x 10^{-8}*
Coefficient		– 5.1406	7.4118	– 1.8403	– 2.0515	15.1755	
p =		*0.0113*	*9.9 x 10^{-8}*	*0.0009*	*0.0785*	*0.0036*	*3.67 x 10^{-9}*
Coefficient		– 5.6789	7.3918	– 1.4979		10.9091	
p =		*0.0064*	*2 x 10^{-7}*	*0.0039*		*0.0182*	***2.96 x 10^{-9}***
Coefficient			7.5427	– 1.5957		2.3250	
p =			*7.5 x 10^{-7}*	*0.0048*		*0.5203*	*1.87 x 10^{-8}*
Coefficient			8.7077			– 5.1726	
p =			*1 x 10^{-7}*			*0.0739*	*0.23 x 10^{-7}*

Table 4.3. Stepwise linear regression analysis of the influence of five variables on observed predator distance. The table shows regression models after variables are removed from the equation in turn, in order of least signficance. P values in the right-hand column are the overall significance levels of each equation.

Regression model	Significance
"***Predator distance***" = 7.39 ***ba*** – 1.50 ***bs*** – 5.68 ***fw*** + 10.91	*p = 2.96 x 10^{-9}*

Table 4.4. Regression model best predicting observed predator distances (*i.e.* with lowest overall p value). ***ba*** = brood age; ***bs*** = brood size; ***fw*** = female weight.

Observed predator distances for each of the 40 females are given in Table 4.5, together with the distance predicted by the regression model presented in Table 4.4. For nine of the hens, there are no data available on age or weight; in these cases I have used the model that takes into account only brood age and brood size, *i.e.* "predator distance" = 7.54*ba* – 1.60*bs* + 2.33, which has an overall significance of 1.87 x 10^{-8}.

Female	Predicted distance	Observed distance
1	5.45	4.5
2	11.12	6.5
3	12.84	22.0
4	18.52	20.0
5*	15.81	10.2
6	25.91	32.0
7	20.23	16.0
8	25.91	29.0
9*	23.36	25.0
10	3.95	4.0
11*	6.68	7.0
12	17.02	23.0
13	11.34	6.4
14	17.02	11.0
15	24.41	38.0
16	18.73	12.0
17*	21.76	35.0
18	8.13	8.0
19	2.45	3.0
20*	12.62	8.6

Female	Predicted distance	Observed distance
21	9.84	6.0
22	15.52	9.5
23	17.23	13.5
24	6.63	2.5
25*	11.03	13.0
26	8.34	5.1
27	21.41	14.5
28*	18.57	10.1
29	-0.55	1.6
30	-0.55	1.5
31	5.13	3.3
32	12.52	9.1
33	6.85	8.7
34*	16.97	15.0
35*	0.29	8.5
36	-2.04	2.0
37	11.03	10.0
38	5.35	9.0
39	2.14	3.2
40	3.85	5.0

Table 4.5. Observed and predicted predator distances for each of the 40 hens tested. Hens marked with an asterisk represent those for which no weight data are available, and hence for which a modified regression model was used (see text for details).

Tables 4.3 and 4.4 demonstrate that under parametric analysis only three of the five variables, brood age, brood size and female weight, appear to significantly influence the intensity of brood defence in peahens. Since few variables have any degree of interaction (Table 4.2), this conclusion agrees with the findings of Table 4.1: the non-parametric analyses presented in that table also show that only the three variables above were significantly correlated with predator distance. The results from both these analyses are used to test the hypotheses presented in Section 4.1.3.

4.3.2 Hypotheses tested

Chick age

The data support the prediction of hypothesis H_2, that peahens invest in brood defence according to the vulnerability of their chicks. The level of defence decreased significantly with increasing chick age (Figure 4.4), and this result was not confounded by female age, female weight or time in season (*i.e.* Table 4.2 shows that none of these variables are significantly correlated with chick age). Although brood age is correlated with brood size

(Table 4.2), brood age maintains a significant relationship with predator distance even when examined within each category of brood size (Figure 4.5).

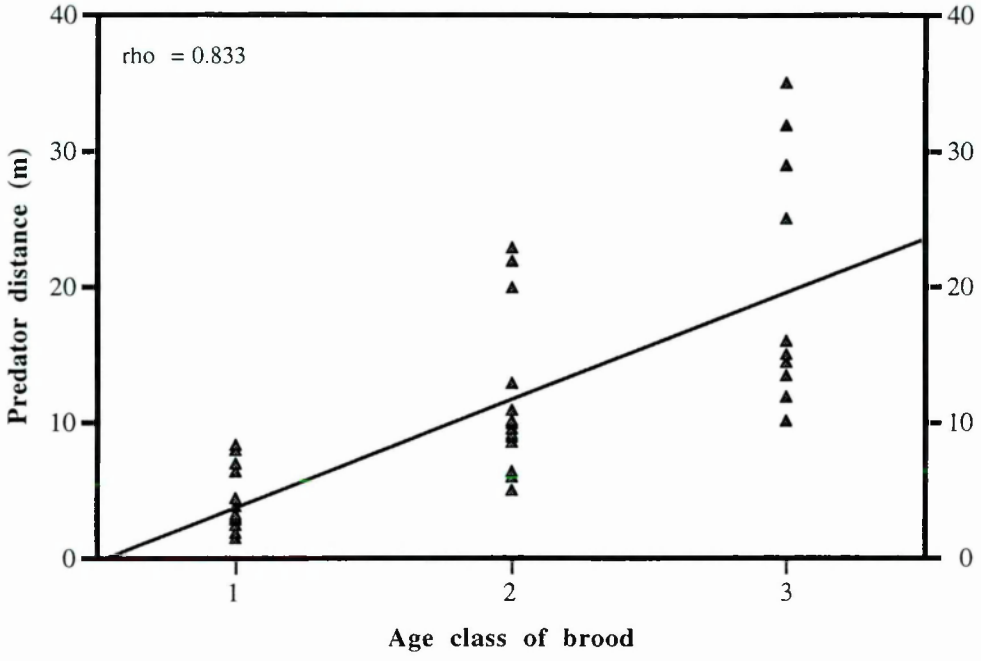


Figure 4.4. Relationship between chick age and "predator distance". Data were analysed using Spearman's rank correlation coefficient, corrected for ties (n = 40, ρ = 0.833, p < 0.00003).

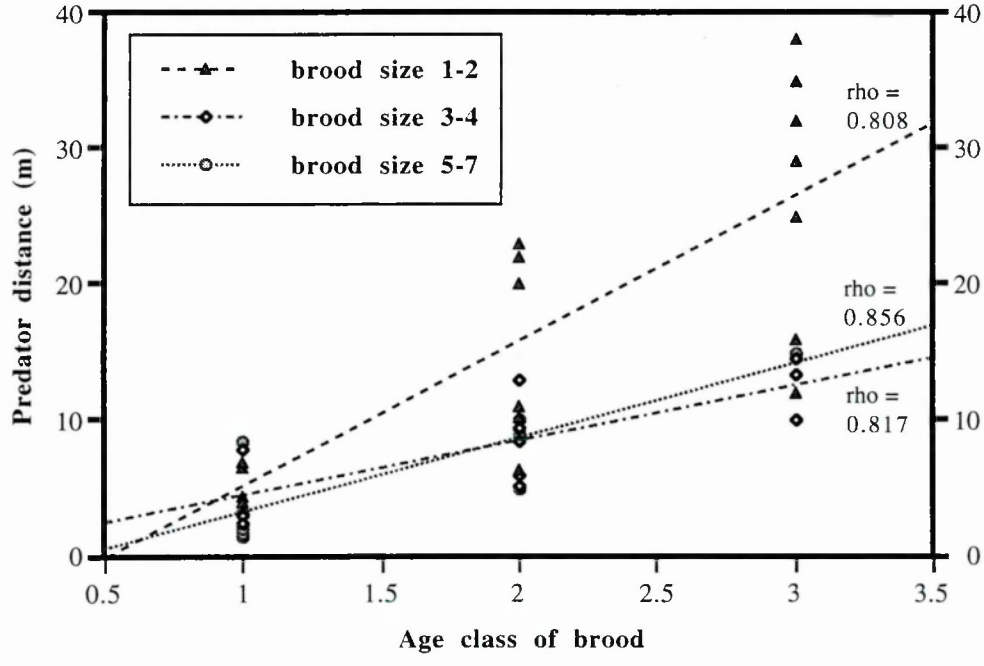


Figure 4.5. Relationship between chick age and "predator distance", for each of three categories of brood size. Data were analysed using Spearman's rank correlation coefficient, corrected for ties: brood sizes 1 - 2, n = 17, ρ = 0.808, p = 0.0006; brood sizes 3 - 4, n = 11, ρ = 0.817, p = 0.0048; brood sizes 5 - 7, n = 12, ρ = 0.856, p = 0.0023.

Brood size

The data support the prediction of hypothesis H_1, that peahens invest more in larger broods which are of a higher total reproductive value. The level of defence increased with increasing brood size (Figure 4.6), and this result was not confounded by female age or weight (Table 4.2). Although brood size is correlated with brood age, brood size maintains a significant relationship with predator distance when examined within the two older categories of brood age, but the relationship is not significant within the youngest brood age category (Figure 4.7). Brood size is also correlated with time of year, and maintains a significant relationship with predator distance only within the mid-season category (Figure 4.8).

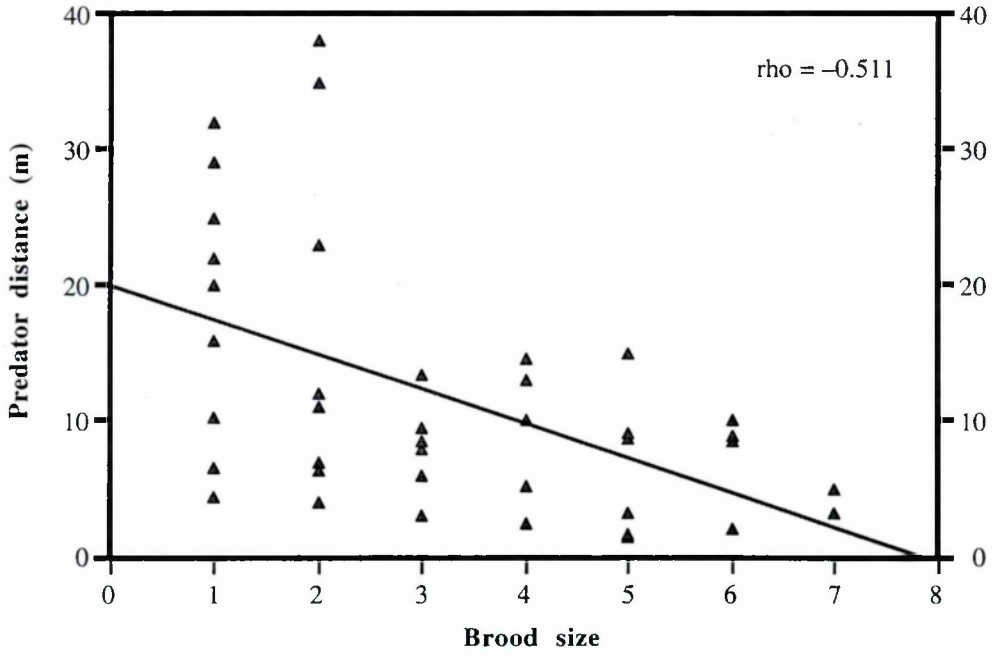


Figure 4.6. Relationship between brood size and "predator distance". Data were analysed using Spearman's rank correlation coefficient, corrected for ties (n = 40, ρ = –0.511, p = 0.0007).

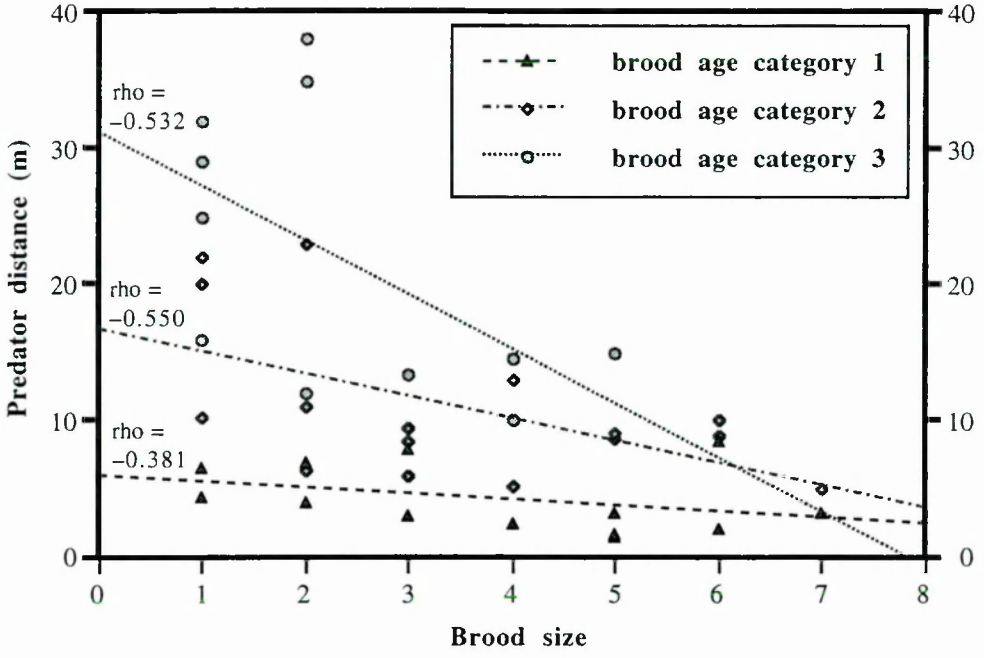


Figure 4.7. Relationship between brood size and "predator distance", for each of three categories of chick age. Data were analysed using Spearman's rank correlation coefficient, corrected for ties: brood age category 1, n = 13, ρ = –0.381, p = 0.0934; brood age category 2, n = 16, ρ = –0.550, p = 0.0166; brood age category 3, n = 11, ρ = –0.532, p = 0.0465.

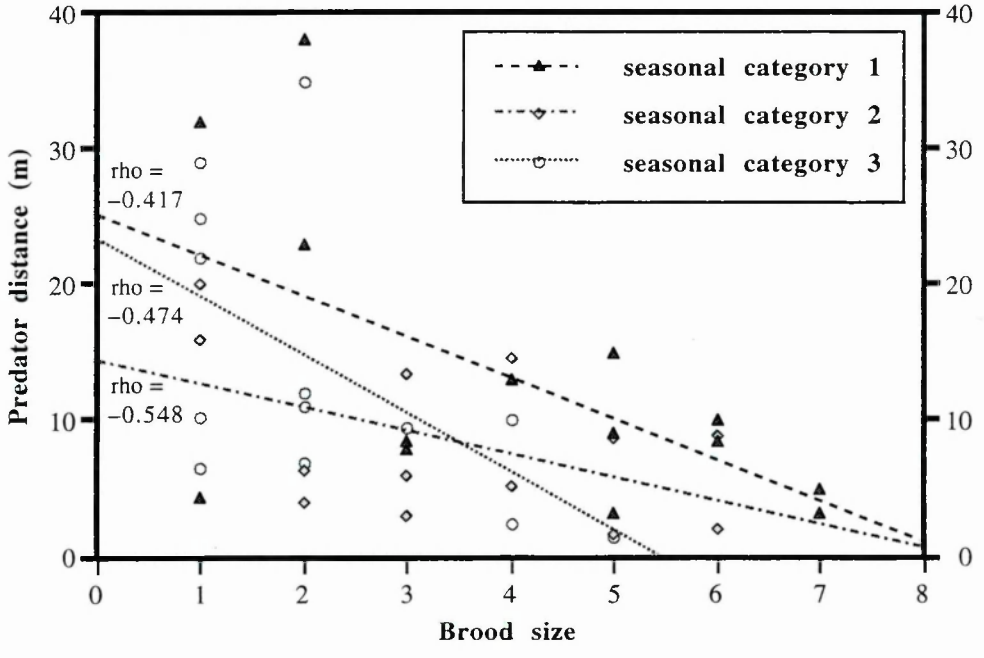


Figure 4.8. Relationship between brood size and "predator distance", for each of three seasonal categories. Data were analysed using Spearman's rank correlation coefficient, corrected for ties: early season, n = 13, ρ = –0.417, p = 0.0749; mid-season n = 14, ρ = –0.548, p = 0.02396; late season, n = 13, ρ = –0.474, p = 0.0505.

Time in season

The data do not support the predictions of either hypothesis H_1, that peahens invest in brood defence in accordance with brood reproductive value, or hypothesis H_2, that they invest according to renesting potential. The observation that there is no significant trend in the level of brood defence over the season (Figure 4.9) supports hypothesis H_0; this may be interpreted either as there being no relation between defence and time in season, or that predator distance is influenced by both brood reproductive value and renesting potential, but in opposite directions.

Time in season is correlated with two other variables, female weight and brood size (Table 4.2). When the relationship between time in season and predator distance is examined within each category of female weight, there was still no significant correlation between time of year and brood defence (Figure 4.10). When the same relationship is examined within each brood size category, there is found to be evidence of an increase in brood defence over the season, but this correlation is significant only for the larger broods (Figure 4.11).

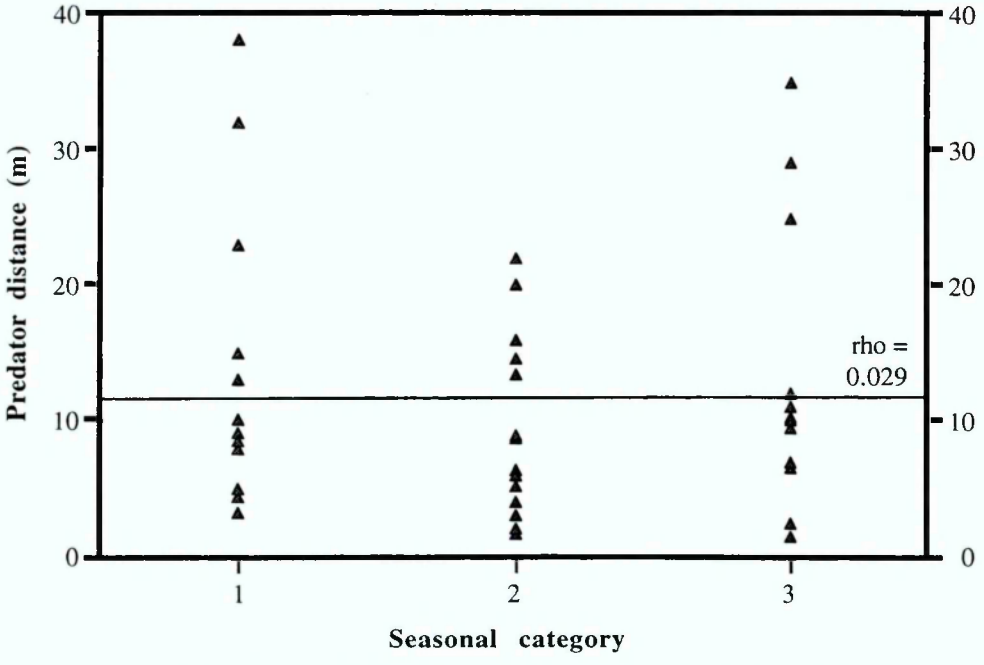


Figure 4.9. Relationship between seasonal category and "predator distance". Data were analysed using Spearman's rank correlation coefficient, corrected for ties (n = 40, ρ = 0.029, p = 0.4286).

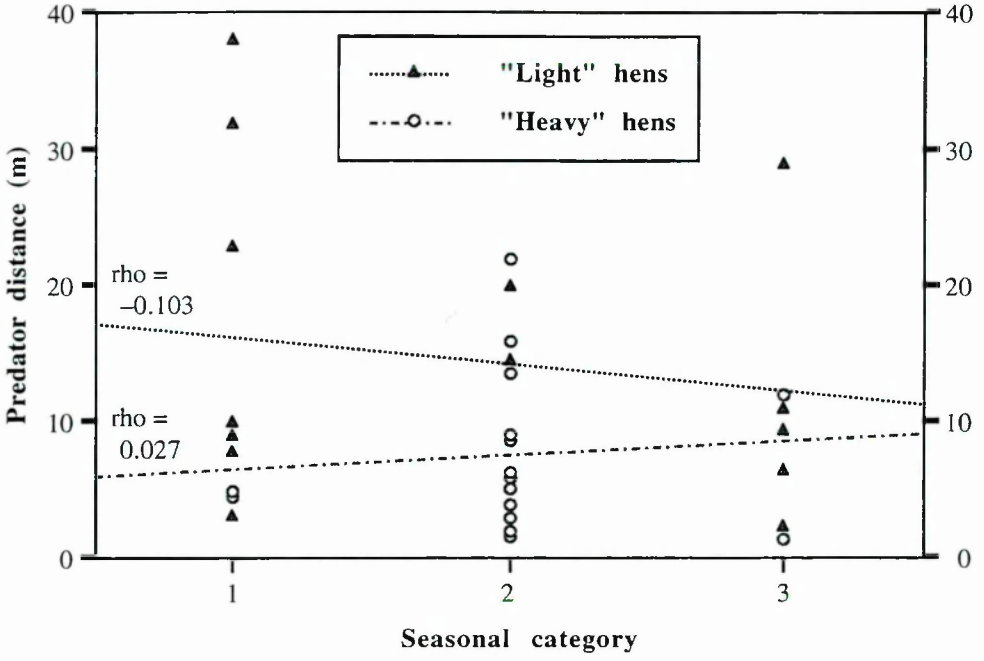


Figure 4.10. Relationship between time in season and "predator distance", for each of two female weight categories. Data were analysed using Spearman's rank correlation coefficient, corrected for ties: "light" females, n = 15, ρ = –0.103, p = 0.3483; "heavy" females, n = 16, ρ = +0.027, p = 0.4562.

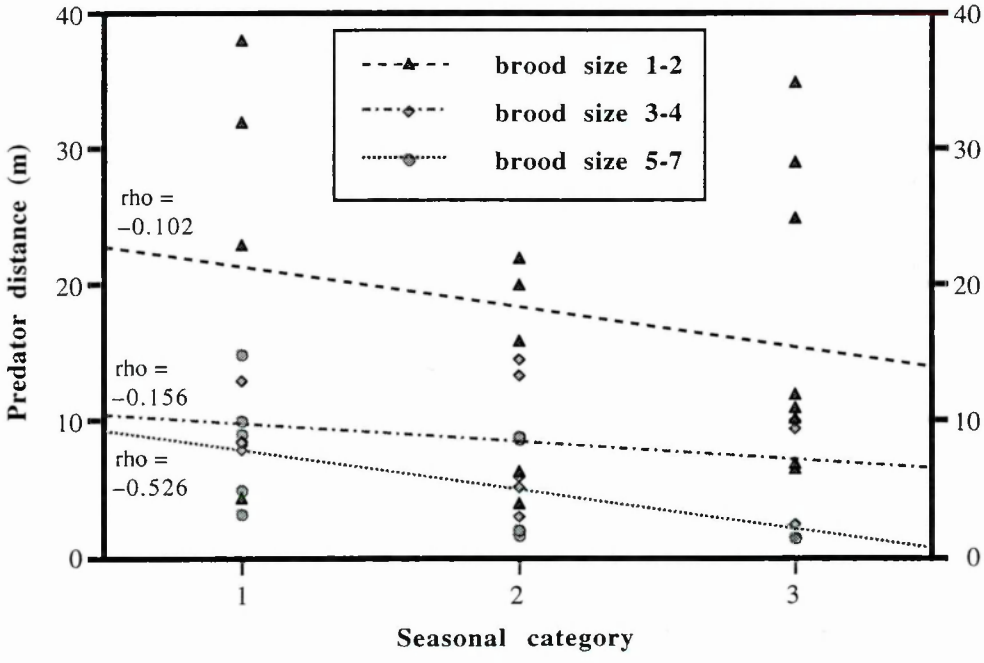


Figure 4.11. Relationship between seasonal category and "predator distance", for each of three categories of brood size. Data were analysed using Spearman's rank correlation coefficient, corrected for ties: brood sizes 1-2, n = 17, ρ = –0.102, p = 0.3409; brood sizes 3-4, n = 11, ρ = –0.156, p = 0.3121; brood sizes 5-7, n = 12, ρ = –0.526, p = 0.0401.

Female age

The data do not support the prediction of hypothesis H_1, that females invest in brood defence according to their own residual reproductive value. There was no significant difference in predator distance between "old" and "young" hens (Figure 4.12), and the result was not confounded by any other variable (Table 4.2). There is some evidence that female age interacts slightly with both brood age and time in season (Table 4.1); however, even within these categories there is no significant relationship between female age and predator distance (Figures 4.13 and 4.14).

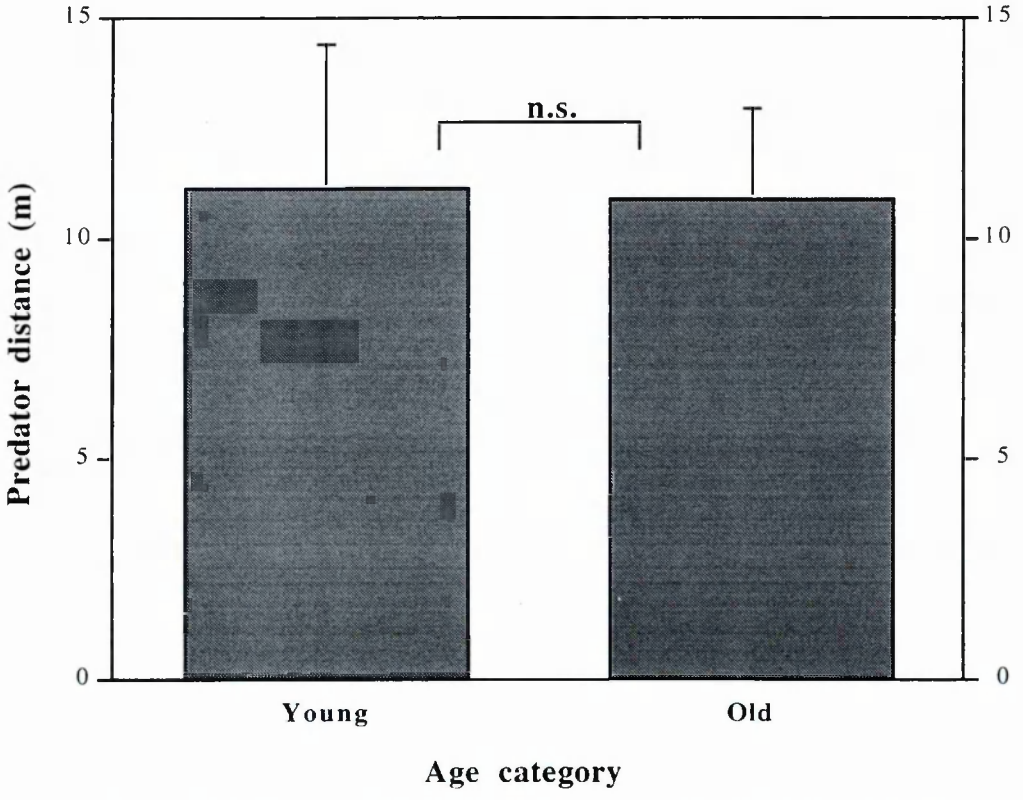


Figure 4.12. Relationship between female age and "predator distance". Error bars represent one standard error of the mean. Data were analysed using a Mann-Whitney U test ($n_1 = 9$, $n_2 = 22$, $U' = 103$, $p = 0.4325$).

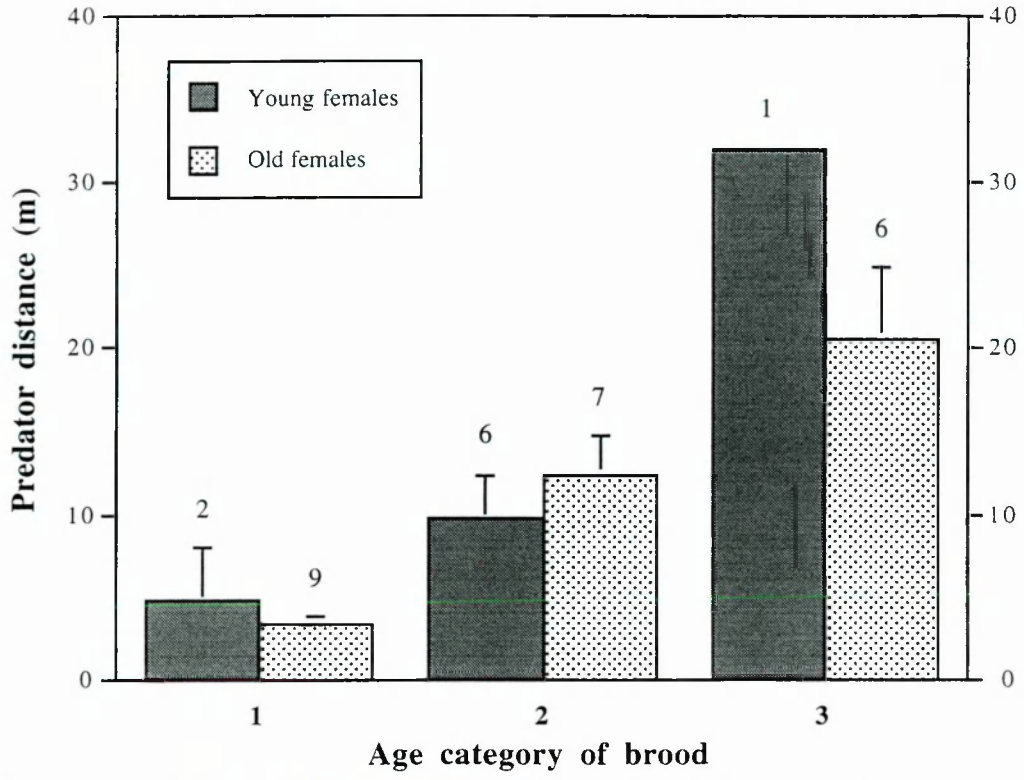


Figure 4.13. Relationship between female age and "predator distance", for each of three categories of chick age. Error bars represent one standard error of the mean; numbers above columns represent individual sample sizes. Data were analysed using Mann-Whitney U tests: brood age category 1, U' = 10, p = 0.4052; brood age category 2, U' = 26, p = 0.2389; brood age category 3, U' = 5, p = 0.1587.

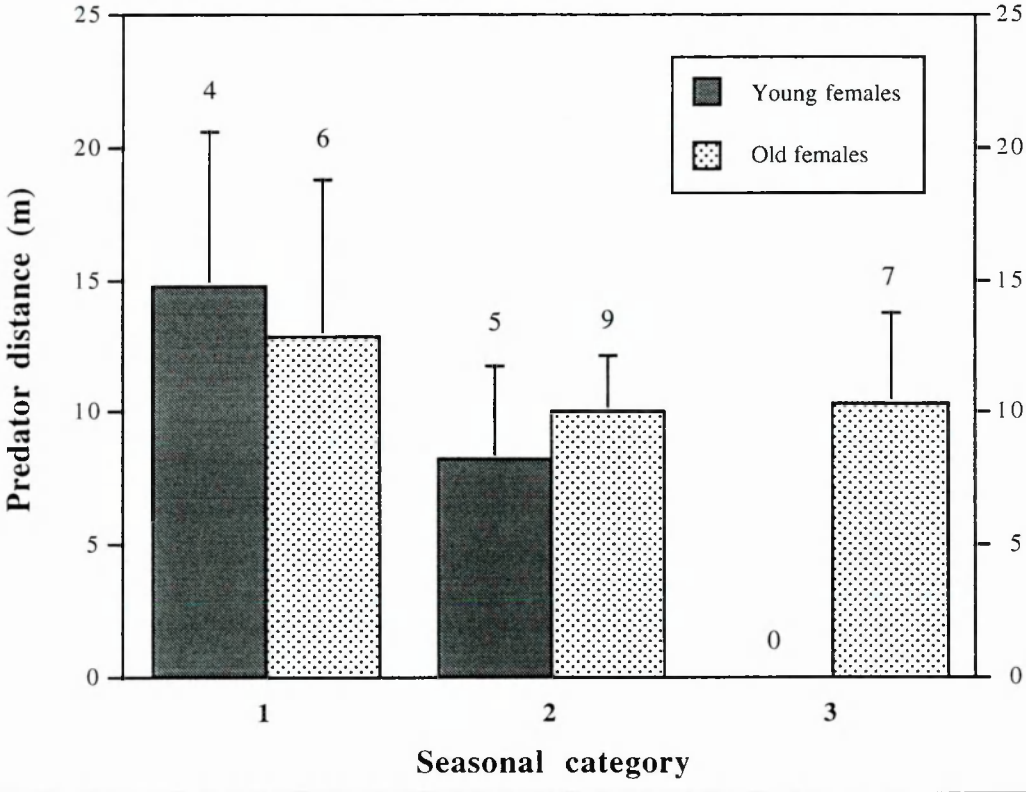


Figure 4.14. Relationship between female age and "predator distance", for each of three seasonal categories. Error bars represent one standard error of the mean; numbers above columns represent individual sample sizes. Data were analysed using Mann-Whitney U tests: early season, U' = 17, p = 0.1423; mid-season, U' = 27, p = 0.2743; late season, statistics not possible.

Female weight

The data support the prediction of hypothesis H_1, that investment in brood defence is constrained by female body condition. "Heavy" females allowed me to approach significantly closer than "light" females (Figure 4.15). The result was not confounded by female age, chick age or brood size, but female weight is correlated with time in season (Table 4.2). However, the relationship between female weight and predator distance is maintained even when examined within each seasonal category (Figure 4.16), although the difference was significant only in mid-season.

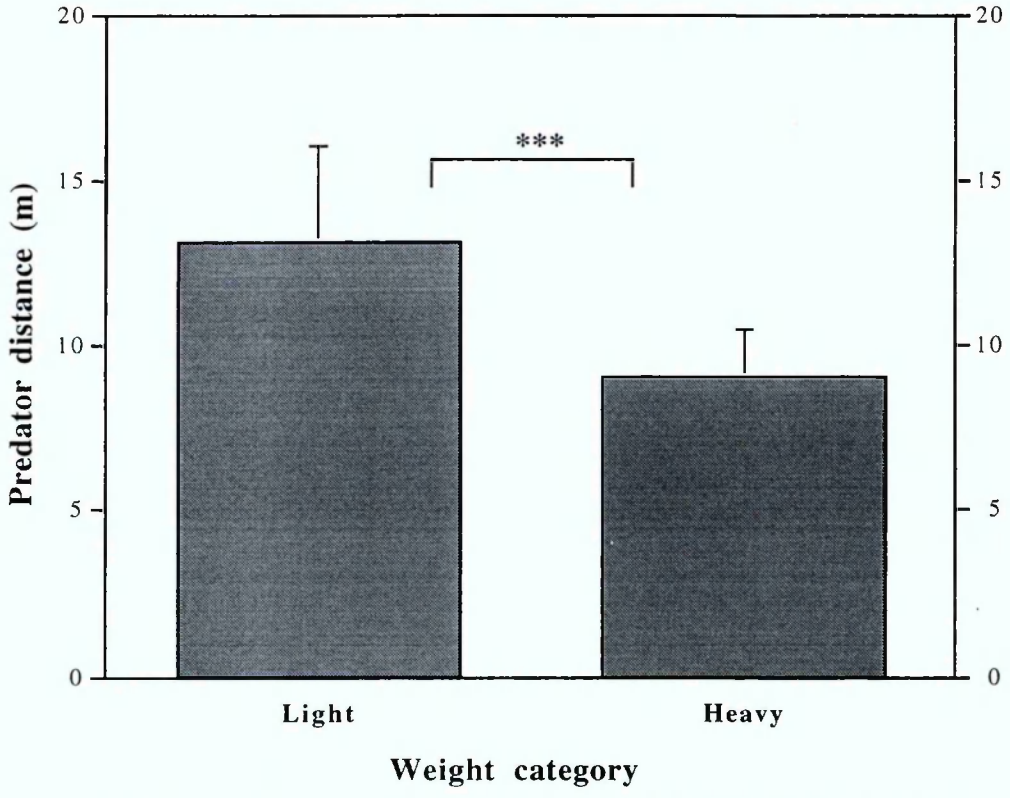


Figure 4.15. Relationship between female weight and "predator distance". Error bars represent one standard error of the mean. Data were compared using a Mann-Whitney U test: $n_1 = 15$, $n_2 = 16$, $U' = 198$, $p = 0.001$.

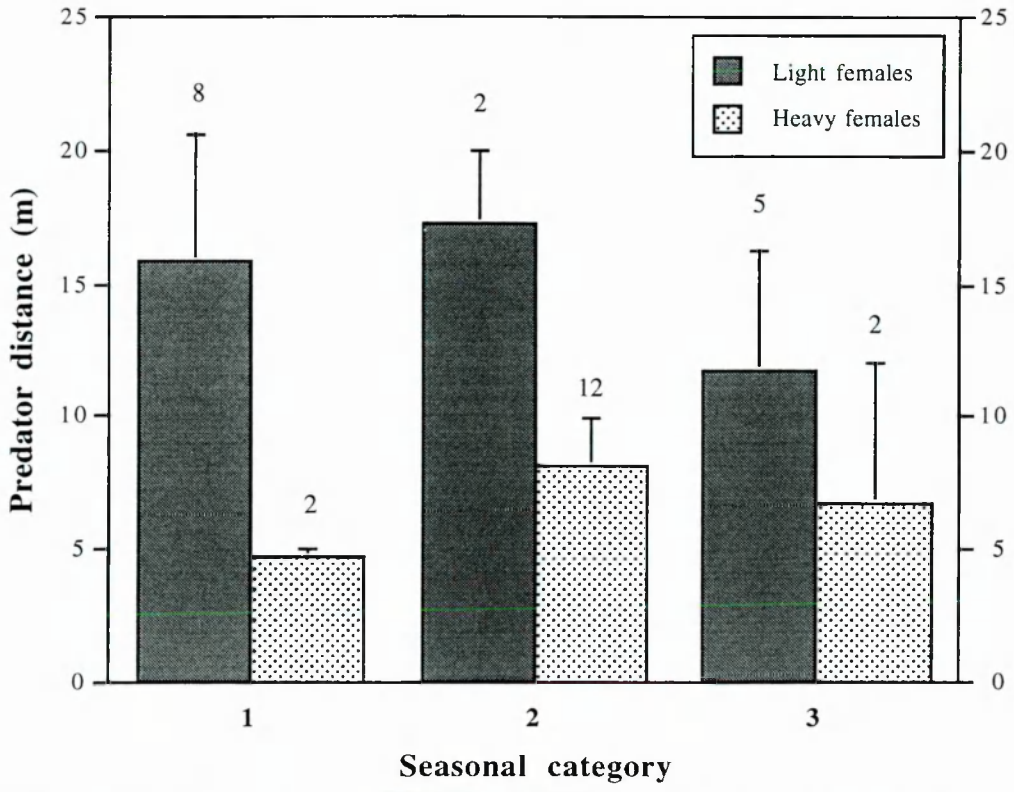


Figure 4.16. Relationship between female weight and "predator distance", within each of three seasonal categories. Error bars represent one standard error of the mean; numbers above the columns represent individual sample sizes. Data were compared using Mann-Whitney U tests: early season, U' = 12, p = 0.1492; mid-season, U' = 21, p = 0.0500; late season, U' = 6, p = 0.3483.

4.4 Discussion and conclusions

The aim of this study was to investigate brood defence in relation to predictions of parental investment theory (Williams 1966a,b; Trivers 1972), which predicts that defence should increase as offspring reproductive value increases, and as parental residual reproductive value declines. In order to eliminate some of the potentially confounding factors which have beset many previous studies (see *e.g.* Montgomerie & Weatherhead 1988), I have examined brood defence in relation to five different parental, offspring and environmental variables.

Chick age

The common observation that parental investment in nest or brood defence changes with chick age has been attributed variously to (a) increasing chick reproductive value (*e.g.* Grieg-Smith 1980; Wiklund 1990a,b), (b) decreasing chick vulnerability, in precocial

species (*e.g.* Simmons 1955; Andersson *et al.* 1980; Brunton 1990), (c) declining renesting potential over the season (*e.g.* Barash 1975; Biermann & Robertson 1981; but see Nur 1983), (d) increased familiarity with the intruder or "predator" (*e.g.* Knight & Temple 1986), and (e) the confounding effects of multiple visits to the same parents (*e.g.* Westmoreland 1989). In this study I have tested each brood only once in a season, thereby removing the problems of (d) and (e). To test between (a), (b) and (c), I measured brood defence with respect both to chick age and to time in season.

The intensity of brood defence by peahens is found to decrease significantly between hatching and fledging, and this result is not confounded by any other factor. This finding supports the "vulnerability hypothesis" (Figure 4.1*c*), which predicts that defence will decline as chicks become increasingly able to scatter at the threat of predation (Harvey & Greenwood 1978). As chicks improve their own response to a predator, the benefits of parental defence will be relatively lower. This can be drawn as a lower benefit curve in the model presented in Figure 4.2, which results in the optimum intensity of brood defence shifting to the left with increasing chick age (Figure 4.17). Thus peahens with older broods invest less in their defence than those with younger chicks.

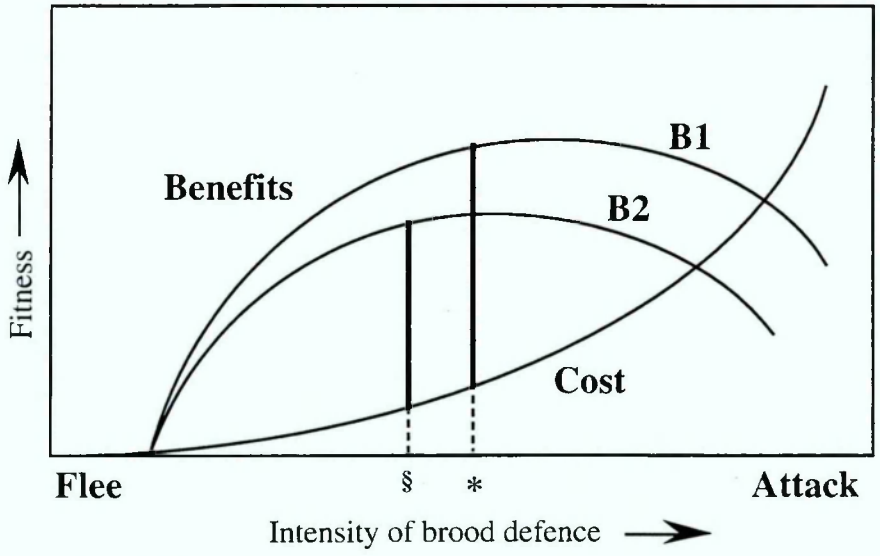


Figure 4.17. Graphical model of defence of a precocial brood, based on the model presented in Figure 4.2. As chicks get older, the benefit of parental defence declines from curve *B1* to curve *B2*, shifting the optimum level of defence to the left, from * to § (see also Montgomerie & Weatherhead 1988).

Brood size

The intensity of brood defence increases with brood size, thus supporting the reproductive value hypothesis, but this result was confounded by the effects of brood age and time in season. Due to natural predation and mortality, brood size declines over the period between hatching and fledging, so that the larger broods tested are likely to be younger than small broods. Similarly, larger broods tend to occur earlier in the season than small ones, and greater defence of larger broods may merely reflect a decline in defence over the season. Nevertheless, the negative correlation between brood size and predator distance was maintained within the two older chick age categories, and was significant in one and nearly significant in two of the seasonal categories.

Although these observations appear to support parental investment theory, that parents should invest more in broods of a higher total reproductive value (Williams 1966a,b; Trivers 1972), the results contrast with more recent theoretical and field studies of brood defence in precocial species. Lazarus & Inglis (1986) demonstrated that the optimal level of an unshared component of parental expenditure, such as brood defence, may differ for parent and offspring, and is expected to depend upon the type of predation and the risk to the parent. In altricial species, total brood loss is the norm, and thus the optimum level of defence is predicted to increase with increasing brood size for both parent and offspring (see *e.g.* Knight & Temple 1986; Wiklund 1990a,b). However, in precocial species, predators commonly take only a single young at a time (see *e.g.* Lazarus & Inglis 1978), and the benefit of defence to the parent is therefore independent of brood size, while the benefit to each individual offspring declines with increasing brood size. The observed level of brood defence in precocial species is thus expected to represent the outcome of this parent-offspring conflict over optimal investment, but in any case intensity of defence is not expected to increase with brood size.

Some studies of brood defence in precocial species apparently support Lazarus and Inglis' (1986) hypothesis, since they report no increase in brood defence with brood size (*e.g.* Lazarus & Inglis 1978; Scott 1980). However, few account for confounding variables such as female quality or experience. Thornhill (1989) observed no relationship between brood

size and defence in precocial red junglefowl *Gallus gallus spadiceus* hens when tested with their natural broods, and suggested that this is because parents adjust clutch sizes to their own individual abilities - *i.e.* a small brood is as valuable to a parent that can only rear a small brood as a large brood is to a parent that can rear a large brood. When he experimentally manipulated brood sizes, he found that larger broods were defended significantly more intensely than small broods, and concluded that females were investing in relation to brood reproductive value.

Natural predators of chicks at Whipsnade generally take single offspring at a time, and defence is not therefore expected to increase with brood size (Lazarus & Inglis 1986). The observed positive correlation is thus initially surprising, but I suggest three possible reasons for this apparent anomaly. Firstly, peahens may simply be investing in brood defence in accordance with the total reproductive value of the brood, even though only a single member of the brood is potentially at risk (*cf.* Thornhill 1989). Secondly, although natural chick predators may take only single chicks, peahens may neverthless regard me as a threat to the entire brood. In cases where entire brood loss is the norm, brood defence is predicted to increase with brood size (Lazarus & Inglis 1986). Thirdly, since brood defence consists not only of staying between a brood and the predator, but also of circling and "shepherding" the chicks away from the threat, it is possible that larger broods require more "collection" than small broods; a female with a large brood may thus allow a predator to approach her more closely.

Time in season

The intensity of brood defence does not increase or decrease significantly over the season, suggesting that either there is no relation between predator distance and either offspring reproductive value or renesting potential, or that both factors influence defence in opposite directions. Time in season is confounded both by female weight and by brood size. Within each category of female weight, the relationship is still non-significant; however, when examined within each brood size category, there is a tendency for brood defence to increase over the season (although the correlation is significant only within large broods).

It is not possible from these results to draw meaningful conclusions about changes in brood defence over the season, since we cannot differentiate between the alternative hypotheses encompassed by H_0 (*i.e.* (a) that there is no relationship, or (b) that both renesting potential and brood reproductive value are influential). Discrimination between these two hypotheses would be very difficult, since renesting potential cannot be experimentally manipulated without affecting brood reproductive value, and *vice versa.*

Female age

Parental investment theory predicts that in species with age-dependent senescence, expenditure should increase with declining residual reproductive value (Williams 1966b); but peahens do not appear to adjust brood defence levels in relation to their own age. These results contrast with those of Thornhill (1989), who found that in red junglefowl *Gallus gallus domesticus* older hens were more defensive than young hens, after controlling for nesting experience. Survivorship has been shown to be age-dependent in domestic chickens (Hutt 1949, cited in Thornhill 1989) and there is some evidence of age-related senescence in junglefowl (Thornhill 1989); however, although peafowl are also members of the Phasianidae, there is no indication of declining fecundity, fertility or survivorship throughout a peahen's lifetime. I suggest that since peahens are long-lived birds, there may well be no significant decline in survivorship until an individual approaches the end of its lifespan, and consequently parental effort should not be expected to increase until residual reproductive value declines rapidly. Data are therefore needed on the parental expenditure of hens of known age throughout their lifetime.

Female weight

Parental expenditure on brood defence is related to female body condition: heavy hens are significantly more defensive than light hens. This relationship is maintained even after controlling for the confounding variable of time in season, although it is significant only in mid-season. These results suggest that levels of brood defence may be determined by physical constraints rather than female residual reproductive value, in common with the findings of Chapter Three.

Heavier females may have a greater chance of successfully defending a brood than light hens. This could lead to a conditional strategy, whereby it is more adaptive for heavy hens to stay and defend their broods, whereas light females should flee earlier in the face of predation and save themselves for future reproductive attempts, even at the risk of losing the current brood. As the cost of defence declines (*e.g.* with increasing female weight), the optimum level of parental expenditure on defence will increase (Figure 4.18); thus heavy hens are more defensive than light hens.

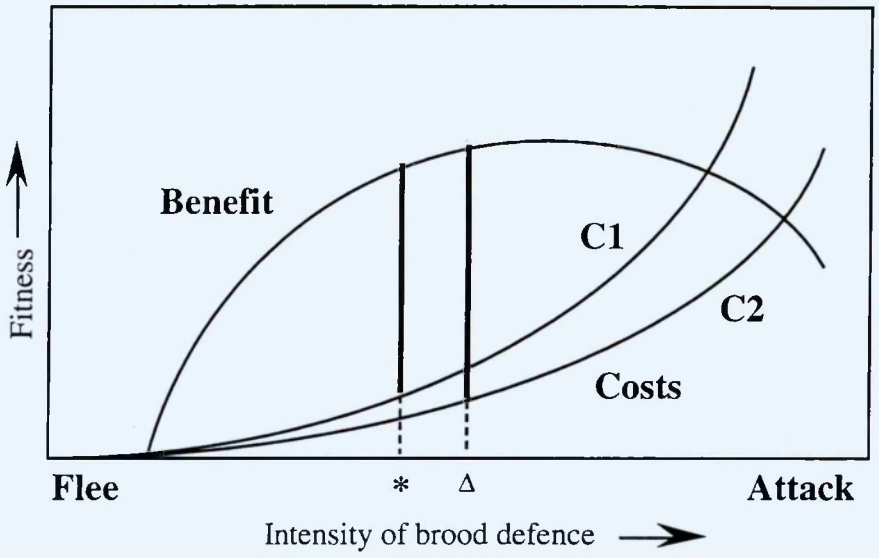


Figure 4.18. Graphical model of defence of a precocial brood, based on the model presented in Figure 4.2. As female weight increases, the cost of parental defence declines from curve *C1* to curve *C2*, shifting the optimum level of defence to the right, from * to Δ (see also Montgomerie & Weatherhead 1988).

Conclusions

The results described here demonstrate that one measure of parental investment in brood defence, "predator distance", is related predominantly to three variables: chick age, brood size, and female weight. Female age and time in season do not appear to have any significant effect on brood defence, although further experiments need to be devised to test whether renesting potential and/or brood reproductive value have any influence on brood defence over a breeding season.

The data suggest that peahens invest in accordance with chick vulnerability rather than individual chick reproductive value, but that expenditure is adjusted to brood size, in contrast with predictions for unshared parental investment in precocial species. Larger broods may

be defended more because of their greater cumulative reproductive value; because they take longer for the hen to collect together; or because hens regard me as a threat to the entire brood rather than individual chicks.

The observation that brood defence is related to female weight rather than age, suggests that investment is governed by constraints rather than female residual reproductive value (see also Chapter Three). A decrease in the costs of defence increases the optimum level of expenditure on defence, whereas a decrease in the benefits (*e.g.* through increasing chick age) decreases optimum defence intensity.

The measurement of five variables has helped to eliminate several potentially confounding factors with respect to hypotheses of brood defence, but sample sizes are too small to produce conclusive results when relationships are examined within categories of each confounding variable. More data are also required on the parental effort of peahens of known age throughout their lifetime, in order to determine whether peahens exhibit age-dependent senescence, and to discover the true nature of the relationship between female residual reproductive value and parental investment.

CHAPTER FIVE

PARENTAL INVESTMENT IN BROODING TIME BUDGETS

5.1 Introduction

5.1.1 Parental investment in brooding

The use of time budgets as a measure of parental investment was introduced in Chapter Three, which investigated the expenditure of time on incubation behaviour patterns. Chapter Four considered investment in chicks, in terms of brood defence, and both chapters examined the relationship between these relative investment levels, and measures of reproductive value and constraints. A similar approach is adopted in this chapter: time budgets are again used to determine variation in parental expenditure, but on broods rather than clutches.

Observed levels of parental expenditure on chicks are likely to be a trade-off between various components of reproductive value, and physiological or environmental constraints; several factors which may influence expenditure were introduced in Section 4.1.1, and will be recapitulated briefly below (for details and sources of reference, refer to Section 4.1.1). One objective of this chapter is to examine the relationship between these factors, and the time allocated to particular behaviour patterns, as determined by time budgets. "Parental" behaviour patterns are defined as those which are significantly more likely to be exhibited by hens with chicks than non-parent hens (*cf.* Section 3.2.2), and these patterns are further categorised as "shared" or "unshared" components of parental investment (Lazarus & Inglis 1978, 1986), depending on context.

One of the most important and widely investigated manifestations of parental care is vigilance, and the particular relationship between vigilance and group size is considered in greater detail in Section 5.1.2; vigilance in peahens is discussed in Section 5.1.3. Observed variation in parental expenditure is used to test predictions arising from a range of hypotheses presented in Section 5.1.4.

- *Parental age.* Reproductive effort theory predicts that in species with age-dependent senescence, investment will increase with parental age, as parental residual reproductive value declines. In contrast, if the probability of mortality does not increase significantly over most of the parent's lifetime, investment may not vary with parental age.

- *Parental quality.* Lower quality parents may be physiologically constrained, and hence be unable to invest as much as high quality parents.

- *Offspring reproductive value.* Parental investment is predicted to increase with chick reproductive value and hence with chick age; similarly, chicks hatched early in the season may be of a higher value than later ones, since they have a greater probability of surviving the next winter.

- *Offspring vulnerability.* Parental investment is predicted to decline at some stage of offspring development as a result of decreasing chick vulnerability (Trivers 1974). Decreasing vulnerability can be expressed as a decline in the benefit of a given parental act as the chick grows older and becomes increasingly self-sufficient (Plate 5.1).

- *Offspring quality.* Expenditure might be expected to be positively correlated with offspring quality; however, higher quality offspring may be less vulnerable (see above).

- *Renesting potential.* All other things being equal, expenditure should increase over the season, as the opportunities remaining for breeding that year decline.

- *Brood size.* The relationship between parental expenditure and brood size will depend upon the nature of the care involved - *i.e.* whether it can be categorised as "shared" or "unshared" (see Section 1.3.3). Lazarus & Inglis (1986) predicted that when parental investment is shared, the optimum level of expenditure (for both parent and offspring) will increase with increasing brood size, within a biologically realistic range of brood sizes (see also Winkler 1987; Montgomerie & Weatherhead 1988). This is because each individual offspring requires a certain minimum level of (shared) investment for successful development, and a larger total number of offspring therefore require a greater

total amount of expenditure (see *e.g.* Lack 1954). The magnitude of parent-offspring conflict is also predicted to increase with brood size (Lazarus & Inglis 1986).

Plate 5.1. As chicks grow older, they become increasingly able to take care of themselves (*e.g.* through increased vigilance for predators).

"Unshared" components of investment might be expected to be independent of brood size, since the benefits of such investment should vary independently of the number of chicks. However, even unshared parental investment may be related to the reproductive value of the brood, if the parent benefits more from a given parental act as brood size increases (*e.g.* Barash 1982). In addition, if the parental act has an anti-predator function (*e.g.* vigilance or brood defence), then the relationship with brood size will depend on whether the predator typically takes the entire brood or a single chick (Lazarus & Inglis 1986).

In altricial species, the brood is confined to the nest site and predators commonly take the entire brood in an attack (Ricklefs 1969; Cody 1971; Brooke & Birkhead 1991). In this case, parental investment is predicted to increase with brood size, although the relationship will depend upon the degree of risk taken by the parent (Lazarus & Inglis 1986). If the parent is killed or injured while defending its brood, its chicks may then have little chance of survival, and the cost of such defence will therefore rise in proportion to the number of chicks. Since the benefits of defence also increase with brood size, it becomes difficult to predict the exact relationship between investment and brood size: there may be a positive, negative or no correlation. Parent-offspring conflict should decline with increasing brood size, since each individual offspring will form a smaller fraction of the total brood, and consequently receive a proportionally greater inclusive fitness gain *via* its siblings, relative to the amount gained directly from the parent (Lazarus & Inglis 1986).

Precocial young are generally mobile from hatching, and can scatter in the face of danger; predators therefore commonly attack precocial young individually (Ricklefs 1969; Welty & Baptista 1988; Brooke & Birkhead 1991). The cost and benefit of defence is thus constant for the parent (termed "fixed-loss": Lazarus & Inglis (1986)), but the benefit for each chick decreases with increasing brood size, since the likelihood that a particular chick will be predated diminishes through prey dilution (Hamilton 1971). Optimum parental investment for the parent is therefore predicted to be independent of brood size, whereas the offspring optimum decreases with brood size,

and parent-offspring conflict over the level of investment will decrease with brood size. For the majority of anti-predator behaviour patterns, the parent is expected to win the conflict over the level of care provided, and expenditure is thus predicted to be unrelated to the number of chicks (Lazarus & Inglis 1986).

The hypotheses produced by Lazarus & Inglis' (1978, 1986) model of shared and unshared expenditure have been extensively tested (goose species appear to be particularly favoured subjects, *e.g.* Lessells 1987; Black & Owen 1989a,b; Turcotte & Bédard 1989; Forslund 1993). Their predictions hold true for many studies, but there are a few exceptions which do not seem to support Lazarus' & Inglis' hypotheses. For example, Forslund (1993) found that vigilance increased with brood size, contrary to the predictions for unshared investment; he suggested however that since larger broods were more dispersed and at greater risk of predation, vigilance would have greater benefits for larger broods (see discussion of Figure 5.1b, below). The converse problem with Lazarus' & Inglis' model was reported by Turcotte & Bédard (1989): they found that shared investment (in the form of relinquishing digging sites to soliciting goslings) did not increase with brood size. They suggested that the magnitude of parent-offspring conflict may be so great (parents spent nearly all their time digging) that expenditure remained at a minimum, irrespective of brood size.

5.1.2 Vigilant behaviour

It was noted in Chapters One and Two that peafowl tend to be fairly gregarious, forming flocks whose size and composition vary according to the season. Group formation has been observed in many bird and mammal species, and the possible causes and functions of grouping have received much attention over the years (*e.g.* Caraco *et al.* 1980; Pulliam & Caraco 1984; Krebs & Davies 1987). The major selective forces promoting flocking are considered to be predation and food, although factors such as thermoregulation, environmental variation, kin selection, population density, dynamics and dominance structure, and the distribution of mates in time and space can also be influential (see Caraco *et al.* 1980; Pulliam & Caraco 1984; Lima & Dill 1990).

Grouping can benefit individuals in the face of predation, through for example earlier predator detection (*e.g.* Pulliam 1973; Lazarus 1979; Dehn 1990), prey dilution (*e.g.* Dehn 1990), confusion (*e.g.* Pulliam & Caraco 1984; McNamara & Houston 1992), the selfish herd principle (Hamilton 1971; but see Pulliam 1973), the edge effect (Lazarus 1978; Inglis & Lazarus 1981; see below), the ability to mob attacking predators (*e.g.* Curio 1978), and in some species reproductive synchrony so that young have increased chance of survival (*e.g.* Patterson 1965). Group formation can enhance foraging efficiency, since larger groups may be able to find food more rapidly, and individuals may gain information about food sources by observing flock neighbours (Dimond & Lazarus 1974; Krebs & Davies 1987).

Potential costs of grouping include increased conspicuousness to predators, intraspecific competition and aggression, and transmission of diseases (Pulliam & Caraco 1984; Krebs & Davies 1987). Trade-offs between the costs and benefits of group formation might be expected to produce an optimal group size. However, optimally sized groups tend to be unstable, since they are joined by individuals from smaller or larger groups (Sibly 1983); in addition, the "optimum" size may vary between different individuals within the group, resulting in a compromise which might be optimal for none of them (Krebs & Davies 1987). The causes and functions of grouping (termed "post-hatch brood amalgamation") in parent peahens will be considered further in Chapter Six; for a general review of living in groups, see Bertram (1978) and Pulliam & Caraco (1984).

Studies on a variety of species have established that individuals are more vigilant when solitary than when in groups, and that vigilance declines with increasing group size (*e.g.* Lazarus 1972; Lazarus & Inglis 1978; Bertram 1980; Lendrem 1982; Westcott & Cockburn 1988; Burger & Gochfeld 1992). This difference has frequently been attributed to the anti-predator benefits of grouping, primarily the "detection effect" (*i.e.* larger groups have an increased chance of detecting a predator, and group members can therefore spend more of their time on non-vigilant behaviour patterns), and the "dilution effect" (*i.e.* each member of a group has a lower chance of being the one attacked) (*e.g.* Pulliam 1973; Bertram 1978, 1980; Lazarus 1979; McNamara & Houston 1992; Forslund 1993). Dehn (1990) integrated these two effects in his "security model", and concluded that both detection and dilution are

important in determining the frequency of vigilance behaviour, but that the relative importance of these two factors changes across group size, with detection providing relatively less benefit as group size increases. The maintenance of a certain level of watchfulness, even in large groups, was investigated by Pulliam (1973), who showed that even a minute increase in vigilance can provide a significant increase in the probability of survival over several predation attempts.

An alternative explanation for the decline in vigilance with group size was given by Lazarus (1978) and Inglis & Lazarus (1981). Birds on the edge of flocks have often been reported to be more vigilant than those in the centre (*e.g.* Inglis & Lazarus 1981; Keys & Dugatkin 1990), and Lazarus and Inglis demonstrated that the decreasing proportion of "edge" birds with increasing flock size produces a lower mean vigilance. In addition, the probability of "false alarms" increases with the number of individuals in the flock; this could be costly if the whole flock responds every time, and consequently a lower level of vigilance could be selected for in larger groups (Lazarus 1990). Alternatively, individuals in larger groups could elevate their response threshold, perhaps only taking flight when a certain number of individuals have raised the alarm. Vigilance as a measure against predation is also affected by distance from protective and obstructive cover (*e.g.* Lima & Dill 1990; Lazarus & Symonds 1992) and potential predators (*e.g.* Lendrem 1983), group composition (*e.g.* Dehn 1990), predation pressure (*e.g.* Forslund 1993) and the type of predation (*e.g.* Lazarus & Inglis 1986).

However, the relationship between vigilance and group size has explanations other than predation. The factors influencing vigilance levels in groups can be divided into three main categories, as follows (see *e.g.* Dimond & Lazarus 1974; Lazarus & Inglis 1978; Pulliam & Caraco 1984; Krebs & Davies 1987; Black & Owen 1989a,b; Lazarus 1990).

(A) Environmental resources, *e.g.* searching for food and shelter, or observing neighbouring birds in order to increase feeding opportunities;

(B) Interactions with conspecifics, *e.g.* maintenance of dominance relationships; monitoring offspring, both in order to retrieve straying young and prevent the infiltration of alien young (this will be related to the offspring's own increasing ability to be vigilant, and

to the development of imprinting); or maintaining contact with breeding partner, although increased calling between partners may decrease the need for visual monitoring;

(C) External dangers (see discussion of anti-predation functions, above).

When considering each of these categories, it should be remembered that there is a subtle difference between "watchful" behaviour patterns used against external dangers, and those falling into categories A and B. In the latter case, individuals are searching for a particular object (*e.g.* food item, or conspecific), whereas the former are being generally vigilant for undefined stimuli (Dimond & Lazarus 1974). One determinant of vigilance levels that does not fit easily into any one of the categories is sexual selection. For example, Dahlgren (1990) found that male partridges *Perdix perdix* spent most of their time vigilant, both pre- and post-hatching, while their partners and chicks foraged; the only significant predictor of female mate choice was found to be the level of male vigilance, and sexual selection can therefore give rise to increased vigilance irrespective of predation pressure, food or conspecific interactions.

Whatever its function, vigilance can be neither perfect, since, for example, animals need to detect, process and respond to a stimulus, nor continuous, since they need to spend time sleeping and feeding. Selection might be expected to operate on the former through development of efficient neural pathways, and on the latter by optimising the time allocated by individuals to vigilance as opposed to other behaviour patterns (Dimond & Lazarus 1974; Lima & Dill 1990; McNamara & Houston 1992).

A general model showing the immediate fitness costs and benefits to an individual of allocating time to vigilance is given in Figure 5.1. This simple model is widely applicable, for example to vigilance by non-parent adults, or to unshared expenditure on vigilance by parents, but it has certain limitations. For example, in cases where vigilance might represent shared investment (*e.g.* if a parent monitors her offspring individually), the cost and benefit functions are more complex and vary for different brood sizes (see Lazarus & Inglis 1986). Nevertheless, it can serve to illustrate how optimum vigilance levels can be affected by changes in the relative costs and/or benefits of vigilance. It is also argued that, since levels

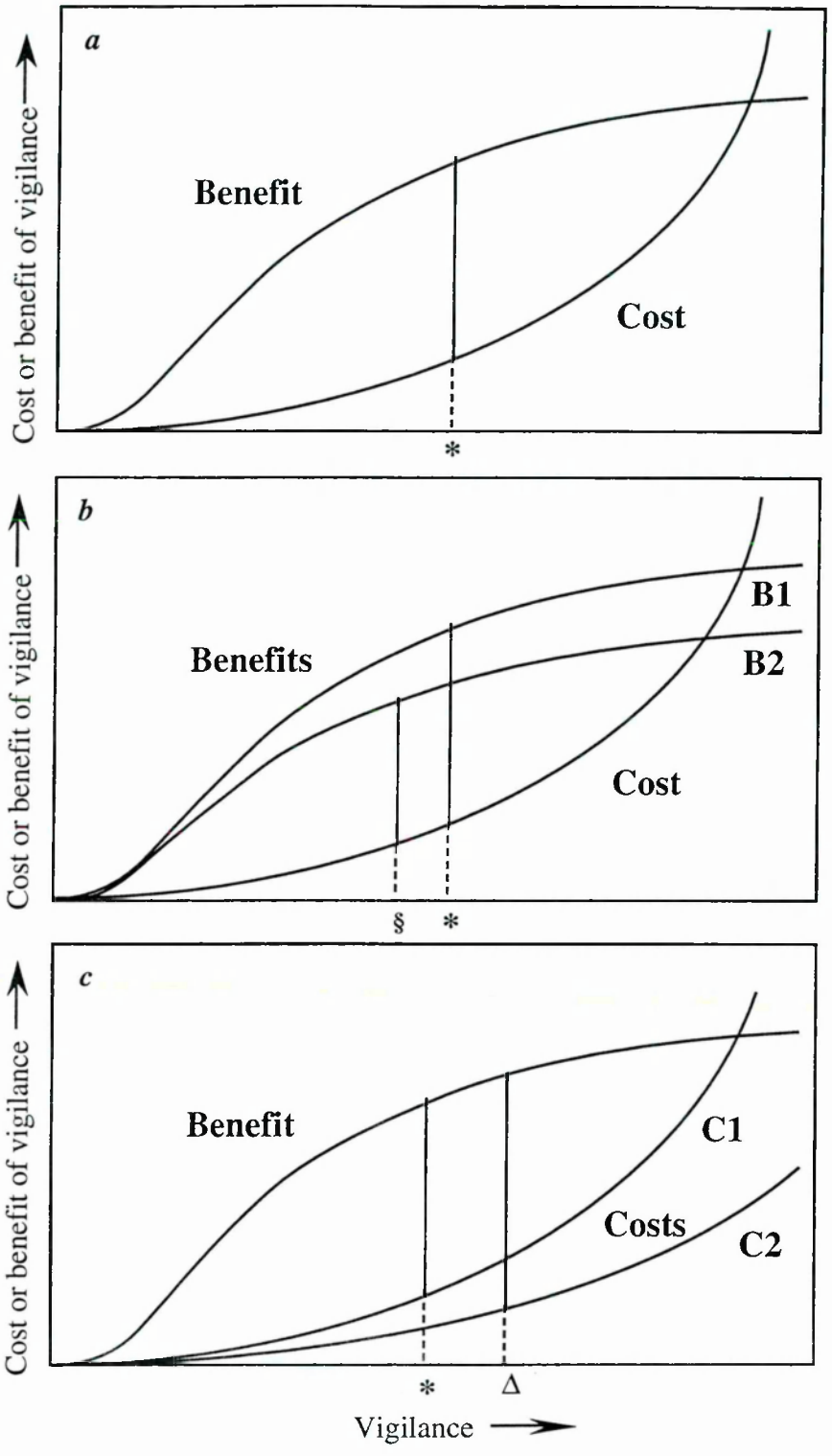


Figure 5.1. *a:* Generalised model for the fitness costs and benefits of vigilant behaviour. The cost curve is concave, since at extreme levels of vigilance the costs of not feeding are assumed to accelerate; the benefit curve is likely to be convex, since the benefit of every additional increase in vigilance will decrease in importance (after *e.g.* Trivers 1974; Lazarus & Inglis 1986; Forslund 1993). *b:* Optimal vigilance levels for different benefit functions: where the benefit of vigilance declines from B1 to B2 (*e.g.* if predation pressure declines, or group size increases), the optimum level is predicted to decrease from * to §. *c:* Optimal vigilance levels for different cost functions: where the cost of vigilance declines from C1 to C2 (*e.g.* food availability increases, so individuals are satiated earlier), the optimum level will increase from * to Δ.

of parental vigilance are generally under the control of the parent, particularly in precocial species, the effects of parent-offspring conflict on this model are minimal. Lazarus & Inglis (1986) predict that unshared investment with an anti-predation function should increase with brood size, if predators usually take the entire brood (*e.g.* in nidicolous species); in this case, the benefit of being vigilant for a large brood (Figure 5.1b: curve B1) is greater than for a small one (curve B2), although the cost remains the same (curve C), and vigilance should increase with brood size. If predators take only single offspring, the costs and benefits of defending large and small broods should be the same (Figure 5.1a).

The common observation that parents are more vigilant than non-parents has sometimes been assumed to provide evidence for the anti-predation function hypothesis (*e.g.* Forslund 1993). However, other explanations are possible: for example, scanning behaviour may be related to the need for parents to search for food for their chicks, or for other gang-broods to join. Differences in vigilance between parents and non-parents in groups are also likely to depend upon the composition of the group (*i.e.* a parent is expected to be relatively more vigilant as the proportion of other parents in the group decreases, since its own offspring form an increasing proportion of the most vulnerable group members), but this factor is rarely acknowledged. One exception is Dehn (1990), who studied vigilance and group size in elk *Alces alces*. He argued that females with young offspring in a group have a greater interest in security than non-parent group members, and are therefore likely to display higher vigilance levels, since they have a greater probability of sustaining loss under attack by a predator. This can be expressed in Figure 5.1b as a greater benefit of vigilance (curve B1), which should lead to higher optimum levels of vigilance by parents.

5.1.3 Vigilance in peahens

Having reviewed a range of possible causes and functions of vigilance, its costs and benefits and its relationship with group size, I now consider the question of vigilance in the Whipsnade population. The initial problem is determining which of the observed behaviour patterns has the function of vigilance. Scanning behaviour (see Section 5.2) appears to be the most likely candidate (see reasons outlined in Chapter Three), and for the purposes of

this study the probability of detecting the stimulus (the benefit), and the decrement in fitness (the cost), were presumed to be proportional to the time allocated to scanning behaviour (however, these assumptions are not always justifiable: see *e.g.* Lazarus 1990; McNamara & Houston 1992).

Three categories of factors influencing vigilance levels were introduced in Section 5.1.2: environmental resources, conspecific interactions, and external dangers (see also Dimond & Lazarus 1974). These categories are further divided to create several alternative functions (see below), and predictions made about the effect of two parameters, (a) solitary *vs.* grouped individuals, and (b) parents *vs.* non-parents, on vigilance levels under each hypothetical function, all other things being equal. The list is by no means exhaustive, but probably includes the factors that are most relevant to the Whipsnade population. The predictions arising from these hypotheses are outlined below, and summarised in Table 5.1.

Potentially important functions of vigilance in peahens at Whipsnade include:

(A) Environmental resources

(i) *Resources for the adult hen* (*e.g.* searching for food, such as seeds, grains, fruits, small animals; or observing other individuals to gain information about food sources). Vigilance is not predicted to differ between solitary and grouped hens, or between parents and non-parents.

(ii) *Resources for chicks* (*e.g.* food, such as insects, grass seeds, grains). Vigilance is predicted to be the same for solitary and grouped hens, but greater for parents than non-parents.

(B) Monitoring conspecifics

(i) *To increase proximity* (*e.g.* to gain from the advantages of grouping). Vigilance is predicted to be greater for solitary than grouped hens, since they are presumably searching for a group to join. No difference is predicted between parents and non-parents, since both are known to form groups or gang-broods.

(ii) *To avoid proximity* (*e.g.* to avoid the costs of aggression, or competition for food. However, since food is abundant and groups tend to be small, competition should be minimal). Vigilance is predicted to be equal for females with and without chicks, but lower for solitary than grouped hens, since the latter would need to monitor their neighbours within a group in order to maintain a minimum distance.

(iii) *Monitoring the position of chicks* (*e.g.* to prevent them straying). Vigilance is expected to be greater for parents than non-parents. Solitary hens are predicted to display similar levels of vigilance to grouped hens, unless the function of chick monitoring is to prevent other chicks approaching their brood, in which case vigilance should be lower for solitary females.

(C) External dangers

(i) *Predators of adult hens* (*e.g.* foxes, badgers, cars). Vigilance is predicted to be greater for solitary than grouped hens, but to be independent of parental status. No difference is expected between "edge" and "centre" birds, since peahen flocks are relatively small and widely spaced, in contrast with *e.g.* goose flocks which can number several thousand (Inglis & Lazarus 1981).

(ii) *Predators of chicks* (*e.g.* foxes, badgers, mustelids, corvids). Vigilance is predicted to be greater for solitary than grouped hens, and for parents than non-parents.

Dehn (1990) demonstrated how vigilance within a group can be affected by its composition, depending upon the proportion of breeding and non-breeding adults and young there are in the group. Group composition may also influence vigilance levels in peahens; however, unlike Dehn's (1990) elk population, the amalgamation of parent peahens with non-parent adults is rare in the breeding season; parents tend to group with parents, and non-parents with non-parents. Analysis of the effect of group composition is therefore difficult, but its potential influence on behaviour should be remembered when comparing the vigilance of females with and without chicks. For example, if parents display greater vigilance than non-parents, a hen with chicks could expect a higher mean vigilance level in a gang-brood than in a group of non-parents, and she may adjust her own vigilance accordingly. This corresponds to Figure 5.1b: the benefits of a hen's vigilance are lower [curve B2] in gang-broods, giving lower optimum vigilance. The phenomenon of "gang-brooding" is discussed in detail in Section 6.2.1, and several selective advantages are suggested for its evolution.

5.1.4 Hypotheses and predictions

Following the hypotheses presented in Section 5.1.3, predictions are made regarding the likely function of vigilance as a parental behaviour pattern (Table 5.1). Subsequent hypotheses relate to various measures of offspring and parental reproductive value, and environmental and physiological constraints, as discussed above. With regard to the predictions, the phrase "females will expend more" implies that peahens will allocate a relatively greater proportion of their time to behaviour patterns categorised as "parental". The hypotheses concerning female age and weight, offspring age and time in season are based upon the hypotheses presented in Section 4.2.3; however, the hypothesis regarding the relationship between parental investment and brood size is considered in greater detail, since shared and unshared components give rise to contrasting predictions.

The function of vigilance in peahens

The hypotheses presented in Table 5.1 do not give rise to entirely mutually exclusive predictions (*e.g.* Bi and Ci); nevertheless they can provide a useful starting point for further analysis.

Hypothesis	Parents *vs.* non-parents	Solitary *vs.* grouped
Ai. Environmental resources: food for adults	P = NP	S = G
Aii. Environmental resources: food for chicks	P > NP	S = G
Bi. Conspecifics: maintain proximity	P = NP	S > G
Bii. Conspecifics: avoid proximity	P = NP	S < G
Biii. Conspecifics: monitor offspring	P > NP	S ≤ G
Ci. Predation: adult predators	P = NP	S > G
Cii. Predation: chick predators	P > NP	S > G

Table 5.1. Predictions arising from the hypotheses presented in Section 5.1.3. Group status: S = solitary, G = grouped; Parental status: P = parent, NP = non-parent. The signs >, <, and = show whether the vigilance of one category of hen is predicted to be greater than, less than, or equal to (respectively) the other category.

Female age

Hypothesis H_1 Peahens invest in a brood according to their own residual reproductive value.

Prediction: Older females will expend more than younger ones.

Hypothesis H_0 Parental investment is not determined by female residual reproductive value.

Prediction: The level of expenditure will not be significantly related to female age.

Female weight

Hypothesis H_1 Parental investment is constrained by female body condition.

Prediction: Heavier hens will expend more than lighter ones.

Hypothesis H_0 Parental investment is independent of female body condition.

Prediction: The level of expenditure will not be significantly related to female weight.

Chick age

Hypothesis H_1 Peahens invest in a brood according to its reproductive value.

Prediction: Females will expend more on older chicks.

Hypothesis H_2 Peahens invest in a brood according to chick vulnerability, or the relative ability of the chick to care for itself.

Prediction: Females will expend more on younger chicks.

Hypothesis H_0 Neither chick reproductive value or vulnerability individually influence parental investment.

Prediction: The level of expenditure will not be significantly related to chick age.

Time in season

Hypothesis H_1 Peahens invest in a brood according to its reproductive value.

Prediction: Females will expend more on earlier broods, which have a higher probability of survival.

Hypothesis H_2 Peahens invest in a brood according to renesting potential.

Prediction: Females will expend more on later broods, since the opportunities available for renesting decline as the season progresses.

Hypothesis H_0 Parental investment is not individually related to either offspring reproductive value or renesting potential.

Prediction: The level of expenditure will not be significantly correlated with time in season.

Brood size

Shared components of investment

Hypothesis H_1 Peahens invest optimally in a brood, maximising net fitness gain, according to the predictions of Lazarus & Inglis (1986).

Prediction: Females will expend more on larger broods.

Hypothesis H_0 Peahens do not invest optimally in relation to brood size.

Prediction: The level of expenditure will not be significantly related to brood size.

Unshared components of investment ("fixed-loss" predation)

Hypothesis H_1 Peahens control the level of unshared parental investment, and invest optimally according to the predictions of Lazarus & Inglis (1986) .

Prediction: The level of expenditure will remain constant with respect to brood size.

Hypothesis H_0 Peahens do not invest optimally in relation to brood size.

Prediction: The level of expenditure will not be independent of brood size.

5.2 Methods

Parental expenditure was investigated by means of time budgets, using the methods described in Sections 2.5.2 and 3.2.2. Each observed behaviour pattern was allocated to one of the eight categories given in Table 5.2. Parents of precocial offspring are commonly assumed not to feed their young, but peahens at Whipsnade were frequently observed holding food in their beaks for their young chicks to peck at (Plate 5.2). Such chick food usually consisted of grass and weed seeds, but females were also seen running to capture flying insects to feed to their chicks.

Hens with broods of various sizes and ages were observed throughout the breeding season, at various times of day (Table 5.3). Additional data included female age and weight, taken from previous capture records, as described in Section 2.2.2. "Non-parent" hens almost

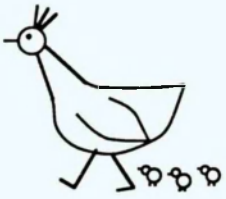
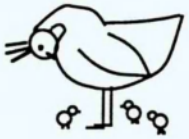
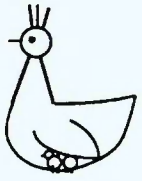
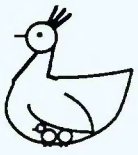
(a) **Scanning (V)**: head high, alert, neck feathers often raised; assumed to have the function of vigilance 	(b) **Standing (S)**: awake but not vigilant 
(c) **Walking (W)** 	(d) **Eating (E)** 
(e) **Feeding chicks (F)**: holding food in beak for chicks to peck at 	(f) **Preening (P)** 
(g) **Sitting vigilant (SV)**: may be brooding chicks 	(h) **Sitting not vigilant (SN)**: eyes open or closed, may be brooding chicks 

Table 5.2. Categories of behaviour used in time budget analysis of peahens with chicks.

certainly included failed breeders, but none of the marked non-parents observed were known to have had eggs or chicks within the previous ten days.

Observations were made between 0600 and 2100 hours; each three-hour period within this time was sampled equally within each week, and observations on each category of female were randomised over the five periods. It was occasionally possible to observe more than one focal animal at a time, by using alternate 30-second point samples of their behaviour patterns. The minimum observation period was 20 minutes; if the focal animal was disturbed (*e.g.* by visitors to the Park) or moved out of sight within this period, the watch was abandoned and the data discarded. Additional information included whether or not the

Plate 5.2. *a:* Female with two newly hatched chicks, holding food in her beak for them to peck at. *b:* Female with three week old chick, pointing to food for her chick.

Variable	Categories	Definition
Female age	"Young" "Old"	≤ 4 years old ≥ 5 years old
Female weight	"Light" "Heavy"	≤ 3.345 kg at previous capture > 3.345 kg at previous capture
Chick age	"Young" "Middle-aged" "Near fledging"	0-5 days old 6-14 days old 15-24 days old
Brood size	"Small" "Medium" "Large"	1-2 chicks accompanying hen 3-4 chicks accompanying hen 5-7 chicks accompanying hen
Group size	"Small" "Medium" "Large"	1 individual 2-3 individuals ≥ 4 individuals
Time in season	"Early" "Mid" "Late"	Up to 14 July 15 July - 14 August 15 August onwards

Table 5.3. Categories of variables used for the analysis of time budgets (for the majority of analyses, actual brood sizes and group sizes were used; the categories shown above refer to pooled sizes when larger sample sizes are required for analysis).

individual was in a gang-brood or group, and the number of adults present (individuals were defined as "grouped" if they were less than ten metres apart: see Section 2.2.1). The brood size (if any) of all members of the group was also recorded as "group composition". If group size changed within the minimum observation period, the focal watch was re-started, but since groups tended to be reasonably consistent in size and composition, this did not seriously disrupt observations. Few data on aggressive interactions and dominance status within groups were recorded (such research is currently being undertaken by M. Hall, Open University).

Records were taken from a total of 98 parent hens and 64 non-parent females over the three year study period; total observation time was 5910 minutes (although some of these observation periods overlapped), and mean observation time per focal watch was 36.48

minutes. The majority of observations were on marked individuals, and unmarked females used for focal watches were observed at different parts of the Park. The problems of non-independent data points should thus be minimised, although some hens were used in more than one year. Several hens were observed more than once during the first three weeks after their broods had hatched, and it was common for broods to decline in size as a result of chick mortality. Only one of these repeated observations from each individual was used for the main analysis, but the additional data could be used for within-subject comparisons of the effects of chick age and brood size on parental behaviour.

5.3 Results

5.3.1 Experiments and observations

The time budgets of parent hens differed from those of non-parent hens: Figure 5.2 shows the overall mean time allocated to each of the behaviour patterns described in Table 5.2, for females with and without chicks.

The time allocated to each of the observed behaviour patterns was compared between parent and non-parent hens. Figure 5.3 shows that there are significant overall differences between parents and non-parents in the way time is allocated to the behavioural categories; data were also compared within each category using Mann-Whitney U tests, in order to determine which behaviour pattern(s) may provide measures of parental expenditure. Parents are found to allocate significantly more time than non-parents to scanning (hereafter termed "vigilance", for the reasons given in Section 5.1.3), walking and feeding chicks. These increases appear to be at the cost of maintenance behaviours, particularly preening, eating, and sitting not vigilant.

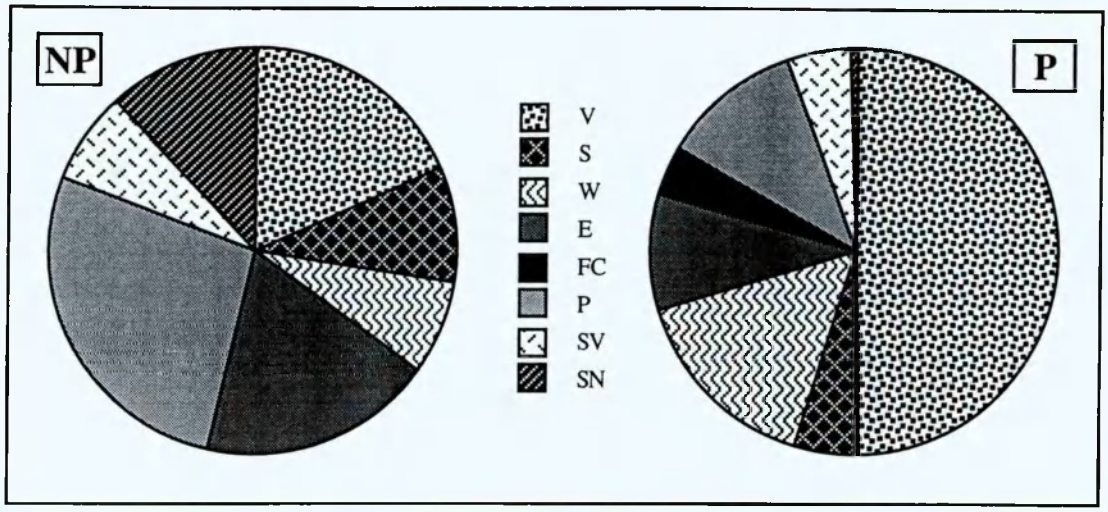


Figure 5.2. Pie charts showing the time budgets of non-parent (NP) and parent (P) females. V = vigilant; S = standing; W = walking; E = eating; FC = feeding chicks; P = preening; SV = sitting vigilant; SN = sitting not vigilant. Analysis of the differences between parents and non-parents is shown in Figure 5.3.

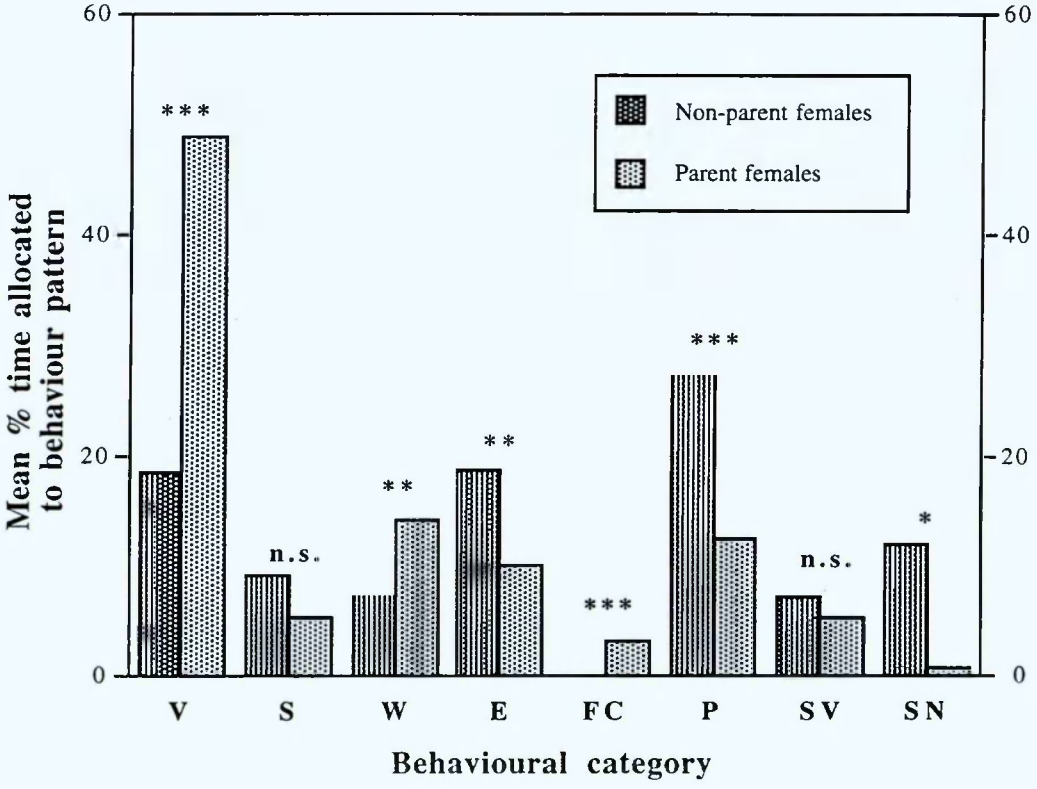


Figure 5.3. Time allocated to each of the eight behavioural categories by females with and without chicks (for abbreviations, see Section 5.2). Differences within categories were analysed using Mann-Whitney U tests; significant differences are denoted by asterisks (*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = $p > 0.05$).

Table 5.4 gives the results of non-parametric tests of the relationships between vigilance, feeding chicks or walking, and the variables listed in Table 5.3. Table 5.5 shows the direction of each relationship between the six variables and the three behavioural patterns. The non-parametric tests do not however account for any interaction between variables that may confound their relationship with the behaviour patterns, and Chi-squared tests and contingency table analyses were therefore used to investigate such interactions (Table 5.6).

	Female age	**Female weight**	**Chick age**	**Brood size**	**Group size**	**Time in season**
Total N	74	74	98	98	98	98
Statistical test	Mann-Whitney U	Mann-Whitney U	Spearman's correl. coeff.	Spearman's correl. coeff.	Spearman's correl. coeff.	Spearman's correl. coeff.
Vigilance Statistic:	U' = 661	U' = 701	ρ = –0.358	ρ = 0.086	ρ = –0.463	ρ = 0.246
Significance:	0.1922	0.4286	**0.00018**	0.1949	**<0.00003**	**0.0071**
Feed chicks Statistic:	U' = 603.5	U' = 688	ρ = –0.388	ρ = 0.259	ρ = –0.014	ρ = 0.147
Significance:	0.4207	0.4840	**0.00006**	**0.0050**	0.4443	0.0710
Walking Statistic:	596	767.5	0.220	0.262	–0.046	–0.051
Significance:	0.4562	0.1841	**0.0143**	**0.0047**	0.3228	0.3050

Table 5.4. Relationships between each of six variables and the proportion of time allocated to vigilance, feeding chicks and walking, by parent hens. Data were compared using Mann-Whitney U tests (for variables with two categories), and Spearman's rank correlation coefficient, corrected for ties (for variables with three or more categories). The resulting statistics and their associated significance levels are given.

Behaviour pattern	Female age	Female weight	Chick age	Brood size	Group size	Time in season
Vigilance	0	0	–	0	–	+
Feeding chicks	0	0	–	+	0	+
Walking	0	0	+	+	0	0

Table 5.5. Direction of the relationships between each of six variables and the proportion of time allocated to vigilance, feeding chicks and walking, by parent hens. "+" indicates a positive correlation, "–" indicates a negative correlation, and "0" indicates no significant relationship ($p > 0.10$).

Variable (No. categories)		Female age (2)	Female wt. (2)	Chick age (3)	Brood size (7)	Group size (8)
Female weight (2)	p	$\chi^2 = 0.357$ 0.5501				
Chick age (3)	p	$\chi^2 = 0.142$ 0.9315	$\chi^2 = 0.034$ 0.9833			
Brood size (7)	p	$\rho = -0.166$ 0.0778	$\rho = 0.179$ 0.0630	$\rho = -0.304$ **0.0012**		
Group size (8)	p	$\rho = -0.088$ 0.2266	$\rho = -0.040$ 0.3669	$\rho = 0.047$ 0.3192	$\rho = -0.115$ 0.1251	
Time in season (3)	p	$\chi^2 = 0.512$ 0.7742	$\chi^2 = 8.627$ **0.0134**	$\rho = -0.080$ 0.2119	$\rho = 0.034$ 0.3669	$\rho = -0.140$ 0.0823

Table 5.6. Interaction among the first six variables given in Table 5.3. The degree of interaction is determined by chi-squared and contingency table analysis, and Spearman's rank correlation coefficient (corrected for ties). Test statistics and associated significance levels are shown, and significant interactions are highlighted in bold.

Table 5.6 shows that there are two highly significant interactions between the variables, and three other p values that suggest there may be some degree of interaction. Young hens appear to have slightly larger broods than old ones; heavy hens also have larger broods and breed significantly earlier than light hens; brood size decreases markedly with chick age, through chick mortality; and large groups tend to occur earlier in the season than small groups. As in Chapter Four, stepwise regression analysis is used to determine which of the variables most influence the time allocated to each parental behaviour pattern (Table 5.7). The regression model of best fit for each behaviour pattern (*i.e.* the models with the lowest p values) are given in Table 5.8.

Both parametric and non-parametric analyses (Tables 5.7 and 5.4 respectively) indicate that observed vigilance levels are influenced by chick age, group size and time in season, while feeding chicks and walking are each correlated with chick age and brood size. The results from both these analyses are used to test the hypotheses presented in Section 5.1.4.

Variable:	Female age	Female weight	Chick age	Brood size	Group size	Time in season	Inter-cept	Signif-icance
Vigilance								
(i) Coeff.	2.9730	3.4282	– 7.8357	– 0.7825	– 4.9259	3.7068	62.1798	
p =	*0.3278*	*0.2553*	$2.7x10^{-5}$	*0.2985*	$2.8x10^{-6}$	*0.0200*	$3.8x10^{-8}$	5.2×10^{-9}
(ii) Coeff.			– 7.3699		– 4.9271	2.9439	70.3409	
p =			$3.6x10^{-5}$		$2.2x10^{-6}$	*0.0456*	$1.7x10^{-24}$	2.9×10^{-10}
Feed chick								
(i) Coeff.	0.0752	0.1382	– 0.8416	0.2270	0.1116	0.3344	3.5512	
p =	*0.8761*	*0.7726*	*0.0011*	*0.0598*	*0.4809*	*0.1839*	*0.0348*	*0.0014*
(ii) Coeff.			– 0.8605	0.2232			4.8684	
p =			*0.0007*	*0.0545*			$3.7x10^{-9}$	$4.7x\ 10^{-5}$
Walking								
(i) Coeff.	0.2178	0.3299	2.4538	1.1508	– 0.0733	– 0.3176	6.5627	
p =	*0.8762*	*0.8119*	*0.0010*	*0.0012*	*0.8728*	*0.6617*	*0.1754*	*0.0082*
(ii) Coeff.			2.4803	1.1615			6.5315	
p =			*0.0007*	*0.0006*			*0.0031*	*0.0002*

Table 5.7. Stepwise multiple linear regression analysis of the influence of six variables on each of three patterns of parental behaviour. The table shows regression models after variables are removed from the equation in turn, in order of least signficance. Two sets of coefficients and p values are given: (i) taking into account all of the variables measured; and (ii) after stepwise regression, using only those variables which give rise to the most significant overall relationship (p value in right-hand column).

Multiple linear regression model	**Significance**
"**Vigilance**" = –7.37**ca** – 4.93**gs** + 2.94**ts** + 70.34	$p = 2.9 \times 10^{-9}$
"**Feed chicks**" = –0.86**ca** + 0.22**bs** + 4.87	$p = 4.7x\ 10^{-5}$
"**Walking**" = 2.5**ca** +1.16**bs** + 6.53	$p = 0.0002$

Table 5.8. Regression model best predicting observed levels of parental behaviour (*i.e.* with lowest overall p value). **ca** = chick age; **bs** = brood size; **gs** = group size; **ts** = time in season.

Relationships within individual categories of potentially confounding variables are analysed using the Mann-Whitney U test, and the Spearman's rank correlation coefficient, corrected for ties. Where several variables are correlated with each other, analysis of predicted

relationships within categories can give rise to a large number of additional relationships, each with a smaller sample size. The more analyses performed on a set of data, the greater the likelihood of obtaining a significant relationship by chance and thereby committing a Type I error. Hence, although the influence of confounding variables should always be considered (see below), it is essential not to overestimate the importance of an unexpected correlation (after all, using a significance level of $\alpha = 0.05$, one result in twenty will be significant by chance).

Each of the above "parental" behaviour patterns may be shared or unshared forms of expenditure, depending both on the nature and context of the care. Vigilance as a defence against predation is normally expected to be unshared: if a predator typically takes the whole brood ("brood loss": Lazarus & Inglis 1986), vigilance levels should increase with brood size; whereas if it takes a single chick ("fixed loss"), levels should be independent of brood size. Alternatively, vigilance may be shared, if for example parents are looking for food for their young, and levels are then predicted to increase with brood size. Feeding chicks is a classic example of shared investment, since the food gathered must be divided between the offspring; both expenditure and parent-offspring conflict are therefore expected to increase with brood size. The parental category of walking is not so easy to classify as shared or unshared. If parent hens are walking to seek out other gang-broods to join, expenditure is predicted to be unshared, and to be independent of brood size; if however they are walking to find food for the chicks, expenditure should be shared, and to increase with brood size. The relationship between each of the "parental" behaviours and brood size will be examined in Section 5.3.2.

5.3.2 Hypotheses tested

Vigilance

The relationships between vigilance and each of the six variables measured are shown in Figure 5.4. Parents and solitary hens are more vigilant than non-parents and grouped hens respectively, which supports only one prediction from Table 5.1; the most likely function of vigilance thus appears to be protection against predation of the chicks (Table 5.9). If this is

the case, then vigilance should be negatively correlated with chick age (young chicks being more vulnerable than older ones), and the data support this prediction.

Hypothesis	Parents *vs.* non-parents	Solitary *vs.* grouped
Ai. Environmental resources: food for adults	P = NP ✘	S = G ✘
Aii. Environmental resources: food for chicks	P > NP ✔	S = G ✘
Bi. Conspecifics: maintain proximity	P = NP ✘	S > G ✔
Bii. Conspecifics: avoid proximity	P = NP ✘	S < G ✘
Biii. Conspecifics: monitor offspring	P > NP ✔	S ≤ G ✘
Ci. Predation: adult predators	P = NP ✘	S > G ✔
Cii. Predation: chick predators	P > NP ✔	S > G ✔

Table 5.9. Predictions arising from the hypotheses presented in Section 5.1.3. Group status: S = solitary, G = grouped; Parental status: P = parent, NP = non-parent. The signs >, <, and = show whether the vigilance of one category of hen is predicted to be greater than, less than, or equal to (respectively) the other category; ✔ indicates that the data agree with the predicted relationship, ✘ that they do not.

Anti-predator behaviour patterns should be independent of brood size if predation typically incurs a "fixed loss", but is expected to be positively correlated with brood size either if "brood loss" is the norm, or if performing the behaviour exposes the parent to a high mortality risk (Lazarus & Inglis 1986). Vigilance is not regarded as a high-risk activity, and predators at Whipsnade generally take a single precocial chick at a time; the neutral relationship between vigilance and brood size therefore again supports the conclusion that it functions to decrease the risk of chick predation.

Chick age is however significantly correlated with brood size, but when examined within each brood size category (1-2, 3-4 and 5-7) the negative relationship between chick age and vigilance is maintained (Spearman's rank correlation coefficient: small broods, $n = 36$, $\rho = -0.337$, $p = 0.0233$; medium broods, $n = 38$, $\rho = -0.420$, $p = 0.0053$; large broods,

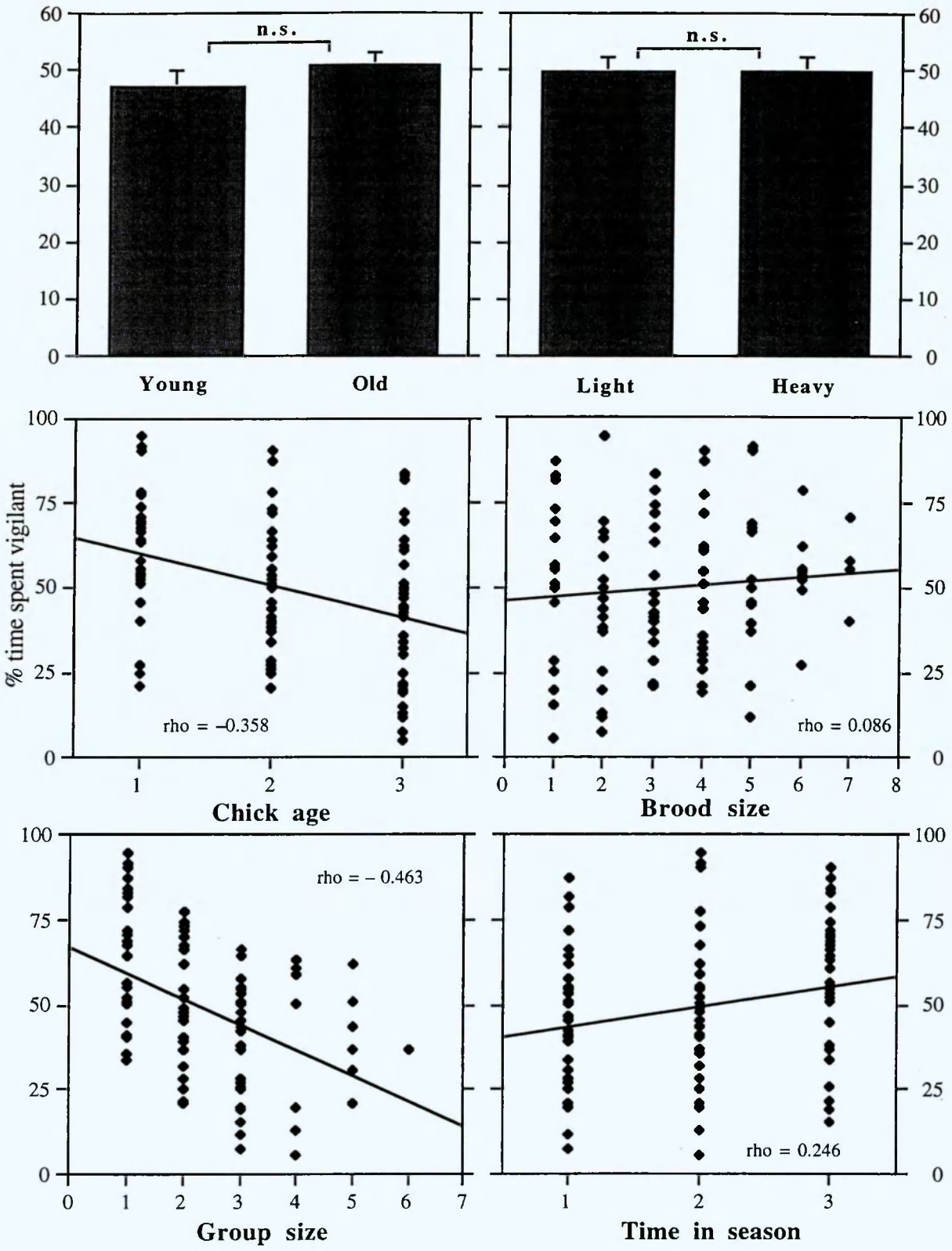


Figure 5.4. Relationship between % time allocated to vigilant behaviour (vertical axes), and each of six reproductive and ecological variables. Data were analysed using Mann-Whitney U test or Spearman's coefficient of rank correlation (female age and weight, N = 74; other variables, N = 98). Significance levels are given in Table 5.4.

n = 24, ρ = –0.682, p = 0.0003). Similarly, within each category of chick age, there exists no significant relationship between brood size and vigilance (Spearman's rank correlation coefficient: young chicks, n = 28, ρ = 0.089, p = 0.3228; middle-aged chicks, n = 36, ρ = –0.112, p = 0.2514; chicks near fledging, n = 34, ρ = –0.024, p = 0.4443).

Brood size is also correlated with female age and female weight (Table 5.6), but within both female age categories there remains no significant relationship between brood size and vigilance (Spearman's rank correlation coefficient: young hens, n = 23, ρ = 0.133, p = 0.2676; old hens, n = 51, ρ = 0.133, p = 0.1736). However, the relationship appears to be confounded by female weight; light hens do not display any correlation between brood size and vigilance, but heavy hens are significantly more vigilant of larger broods (Spearman's rank correlation coefficient: light hens, n = 36, ρ = –0.136, p = 0.2119; heavy hens, n = 38, ρ = 0.308, p = 0.0307).

As mentioned above, solitary females are significantly more vigilant than grouped hens (Figures 5.4 and 5.5). The proportion of time allocated to vigilance also appears to decline with group size, although the "corporate vigilance" (the probability that at least one individual in the flock is vigilant*) increases with flock size. It appears that individual hens can benefit by joining a group not only from a reduction in their individual costs of vigilance, but from increased safety through the higher probability of predator detection.

Peahens do not appear to invest in vigilance in relation either to their own residual reproductive value or to their condition. There is however some indication that female age may be confounded by brood size (Table 5.6), and comparisons within each brood size category show that older hens are more vigilant than young hens in all three categories, but the relationship is significant only in the middle brood size category (Mann-Whitney U test: small broods, n_1 = 5, n_2 = 19, U = 41, p = 0.3228; medium broods, n_1 = 10, n_2 = 20, U = 62, p = 0.0473; large broods, n_1 = 8, n_2 = 12, U = 41, p = 0.2946).

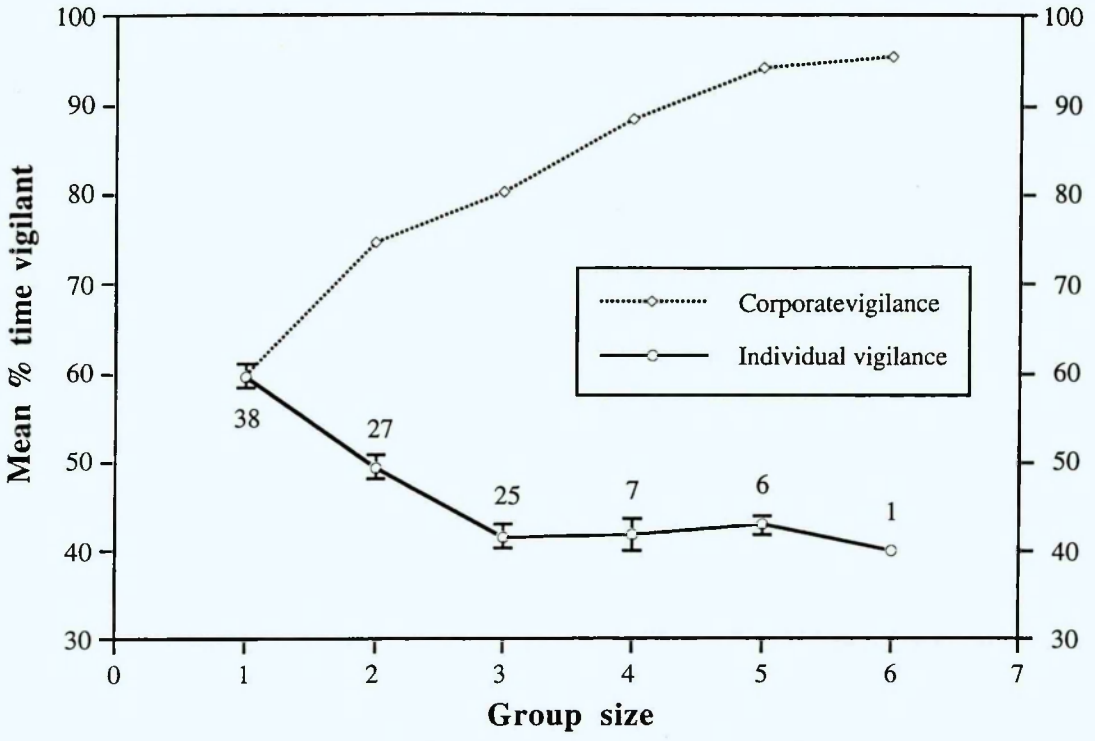


Figure 5.5. Mean observed individual vigilance (±standard error) and theoretically derived corporate vigilance of birds in gang-broods of different sizes (see text for details). Numbers above points refer to sample sizes.

Female weight is also slightly correlated with brood size, and significantly with time in season. Within each brood size and seasonal category, however, there exists no significant relationship between female weight and vigilance (Mann-Whitney U test, within brood size categories: small broods, $n_1 = 13$, $n_2 = 11$, $U = 60.5$, $p = 0.2611$; medium broods, $n_1 = 16$, $n_2 = 14$, $U = 99$, $p = 0.2946$; large broods, $n_1 = 7$, $n_2 = 13$, $U = 33$, $p = 0.1611$. Mann-Whitney U test, within seasonal categories: early season, $n_1 = 6$, $n_2 = 14$, $U = 24$, $p = 0.0681$; mid-season, $n_1 = 7$, $n_2 = 19$, $U = 44$, $p = 0.0968$; late season, $n_1 = 23$, $n_2 = 6$, $U = 68$, $p = 0.4801$).

Vigilance increases significantly over the breeding season, although the effect of season is much less important than that of chick age or group size (Tables 5.4 and 5.7). This provides evidence for the hypothesis that females are investing in their offspring in accordance with

* "Corporate vigilance" is calculated assuming that peahens raise their heads to scan randomly, and independently from each other. The probability that at least one individual in a flock is vigilant is equivalent to 1 – the probability that none of them are vigilant, and is calculated using the formula $1 - (100 - x)^n$, where x is the mean individual vigilance in a group of n birds (see Bertram (1980) for an alternative method).

renesting potential, rather than chick reproductive value. However, female weight is correlated with time in season, and is therefore a potentially confounding factor. The significant relationship between vigilance and time in season is maintained within light hens (Spearman's rank correlation coefficient: $n = 36$, $\rho = 0.376$, $p = 0.0122$), but is non-significant within heavy hens (Spearman's rank correlation coefficient: $n = 38$, $\rho = 0.131$, $p = 0.2119$). The implications of this will be discussed in Section 5.4.

Feeding chicks

Figure 5.6 and Table 5.7 show how the proportion of time allocated to feeding chicks varies in relation to several ecological and life history variables.

Feeding behaviour does not appear to be related to either female age or weight, suggesting that hens are not investing in accordance with their own residual reproductive value, nor with the constraints imposed by their own body condition. Female age is correlated with brood size (Table 5.6), but even when examined within each brood size category, there is no significant relationship with chick feeding (Mann-Whitney U test: small broods, $n_1 = 5$, $n_2 = 19$, $U = 42.5$, $p = 0.3594$; medium broods, $n_1 = 5$, $n_2 = 10$, $U = 22$, $p = 0.3557$; large broods, $n_1 = 8$, $n_2 = 13$, $U = 43.5$, $p = 0.2676$).

Female weight is correlated with both brood size and time in season, but within each of these categories there is no significant relationship with chick feeding (Mann-Whitney U test, brood size: small broods, $n_1 = 13$, $n_2 = 11$, $U = 57.5$, $p = 0.2090$; medium broods, $n_1 = 16$, $n_2 = 14$, $U = 104.5$, $p = 0.3783$; large broods, $n_1 = 7$, $n_2 = 13$, $U = 42.5$, $p = 0.4052$. Mann-Whitney U test, time in season: early season, $n_1 = 6$, $n_2 = 14$, $U = 35$, $p = 0.2810$; mid-season, $n_1 = 7$, $n_2 = 19$, $U = 47$, $p = 0.1292$; late season, $n_1 = 23$, $n_2 = 6$, $U = 61.5$, $p = 0.3446$).

Peahens spend significantly more time feeding young chicks than older chicks, which supports the hypothesis that they are investing in accordance with the chick's increasing ability to care for itself, rather than its reproductive value. Chick age is significantly correlated with brood size, but within each brood size category the relationship between

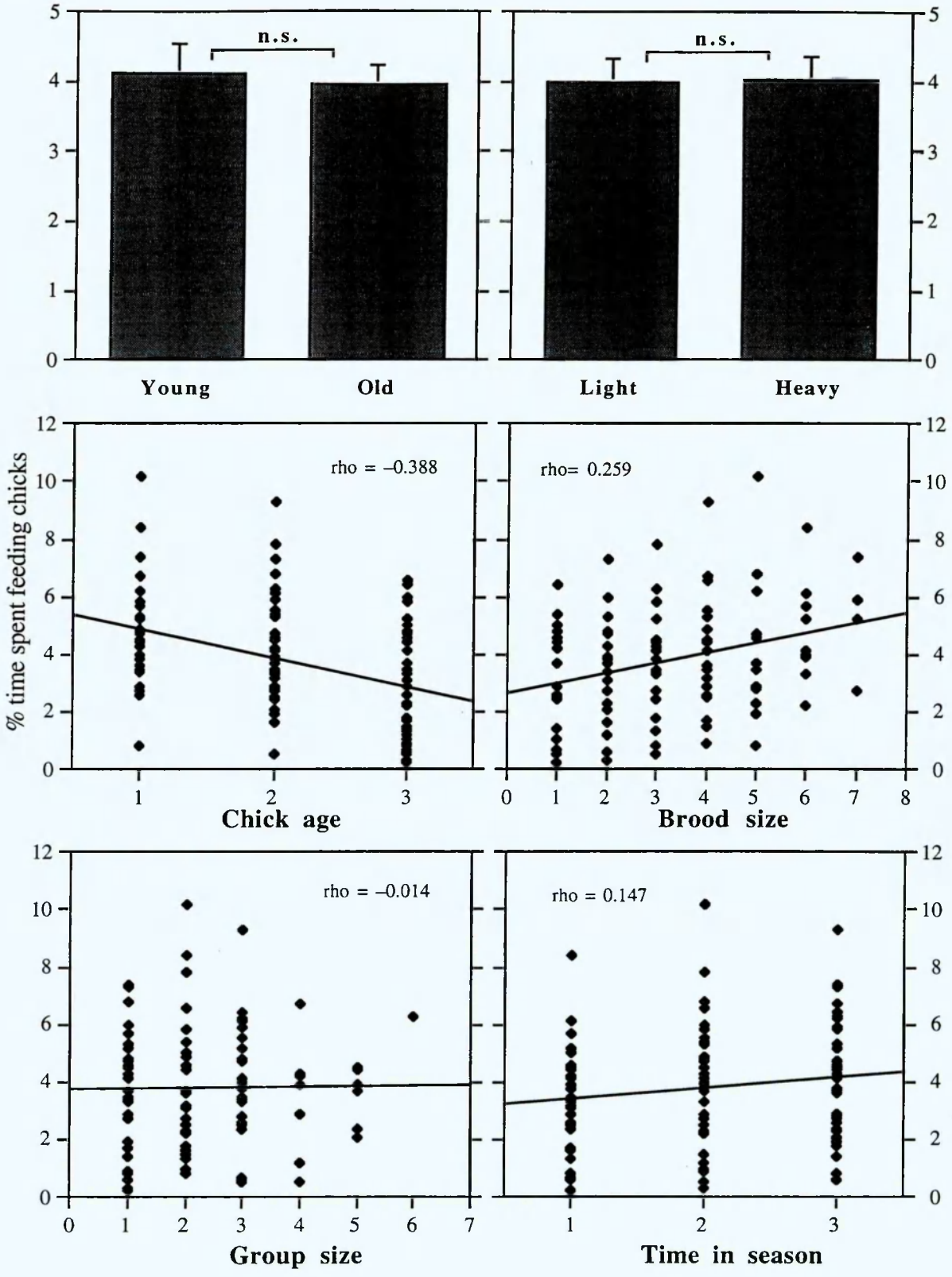


Figure 5.6. Relationship between % time allocated to feeding chicks (vertical axes), and each of six reproductive and ecological variables. Data were analysed using Mann-Whitney U test or Spearman's coefficient of rank correlation (female age and weight, N = 74; other variables, N = 98). Significance levels are given in Table 5.4.

chick age and feeding behaviour is maintained (Spearman's rank correlation coefficient: small broods, n = 36, ρ = –0.320, p = 0.0294; medium broods, n = 38, ρ = –0.378, p = 0.0107; large broods, n = 24, ρ = –0.436, p = 0.0146).

The proportion of time allocated to feeding chicks increases with brood size, thus supporting the prediction for shared parental investment. However, this result is confounded by chick age, since the relationship persists only within the youngest chick age category (Spearman's rank correlation coefficient: young chicks, n = 28, ρ = 0.456, p = 0.0089; middle-aged chicks, n = 36, ρ = 0.111, p = 0.2514; chicks near fledging, n = 34, ρ = 0.202, p = 0.1190). Similarly, female age and female weight appear to be confounding variables, since the relationship is non-significant within both female age categories and both female weight categories (Spearman's rank correlation coefficient, female age: young hens, n = 23, ρ = 0.147, p = 0.2451; old hens, n = 51, ρ = 0.180, p = 0.1020. Spearman's rank correlation coefficient, female weight: light hens, n = 36, ρ = 0.091, p = 0.2946; heavy hens, n = 38, ρ = 0.247, p = 0.0668).

Group size does not appear to influence the time spent feeding chicks, which suggests that gang-brood size does not increase inter-brood competition for food. Although simple non-parametric analysis suggests that there may be some relationship between time in season and chick feeding (Table 5.4), more rigorous multivariate analysis shows that feeding behaviour is influenced significantly only by chick age and brood size, and that time in season has no significant effect. Time in season is correlated with female weight (Table 5.6), but there is no significant relationship between season and feeding in either female weight category (although there is a slight trend for light hens to increase their expenditure over the season) (Spearman's rank correlation coefficient: light hens, n = 36, ρ = 0.248, p = 0.0708; heavy hens, n = 38, ρ = 0.141, p = 0.1949). These results suggest that peahens are not investing in relation either to chick reproductive value or renesting potential; however, it is possible that both factors are influencing expenditure, but in opposite directions. Renesting potential would therefore seem to be the more important influence, since chick feeding tends to increase over the breeding season.

Walking

Figures 5.2 and 5.3 show that parents spend significantly more time walking than non-parents, and "walking" is therefore designated a measure of parental expenditure. However, the function of walking, and how it may benefit the brood or parent, is less easy to determine. As a simple measure of investment, we can predict how time spent walking with a brood should vary with respect to various ecological and life-history variables (see Section 5.1.4); but when considering the relationship between walking and brood size, the function of walking is important as it determines whether the behaviour is a shared or unshared component of parental investment (see below).

Neither female age nor female weight significantly influence the time a parent spends walking (Table 5.7, Figure 5.7). Both variables are correlated with brood size (Table 5.6), but there is no significant relationship between walking and either female age or weight within each brood size category (Mann-Whitney U test, female age: small broods, $n_1 = 5$, $n_2 = 19$, $U = 39.5$, $p = 0.2843$; medium broods, $n_1 = 5$, $n_2 = 10$, $U = 22$, $p = 0.3557$; large broods, $n_1 = 8$, $n_2 = 13$, $U = 45$, $p = 0.3050$. Mann-Whitney U test, female weight: small broods, $n_1 = 13$, $n_2 = 11$, $U = 48.5$, $p = 0.0918$; medium broods, $n_1 = 16$, $n_2 = 14$, $U = 104.5$, $p = 0.3783$; large broods, $n_1 = 7$, $n_2 = 13$, $U = 34$, $p = 0.1814$).

Female weight is also correlated with time in season (Table 5.6), and only in the early and mid-season categories is there no relationship between walking and female weight; in late season, heavy females spend significantly less time walking with their broods than light females (Mann-Whitney U test: early season, $n_1 = 6$, $n_2 = 14$, $U = 39$, $p = 0.4013$; mid-season, $n_1 = 7$, $n_2 = 19$, $U = 57$, $p = 0.2912$; late season, $n_1 = 23$, $n_2 = 6$, $U = 34$, $p = 0.0297$). None of these results support the hypotheses that peahens are investing in accordance with their own residual reproductive value or condition, and the last relationship is significant in the direction opposite to that predicted.

Figure 5.7 shows that time spent walking increases with chick age. The relationship is however confounded by brood size; in small and large broods there is a positive but non-

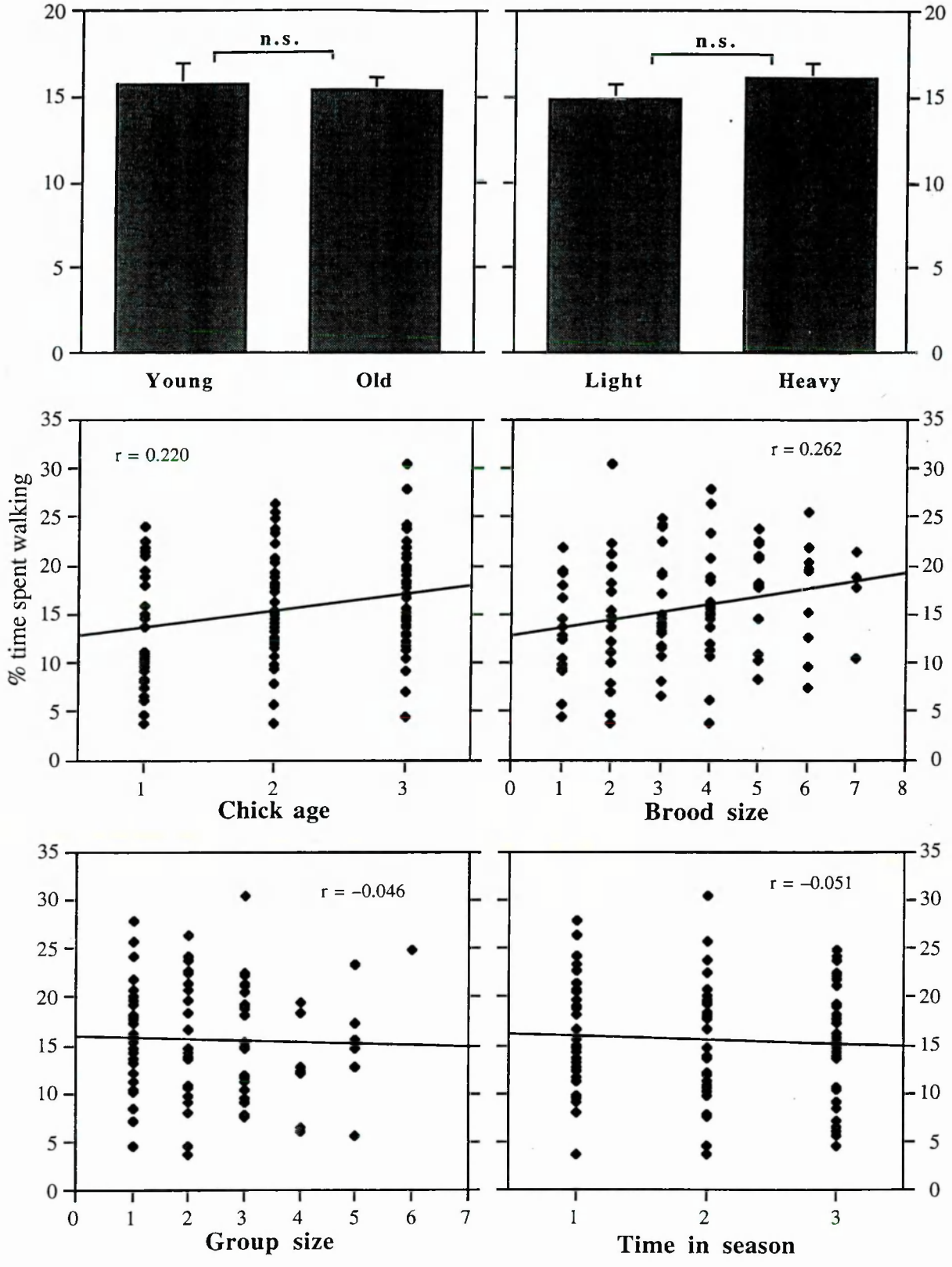


Figure 5.7. Relationship between % time allocated to walking (vertical axes), and each of six reproductive and ecological variables. Data were analysed using Mann-Whitney U test or Spearman's coefficient of rank correlation (female age and weight, N = 74; other variables, N = 98). Significance levels are given in Table 5.4.

sigificant correlation between chick age and walking, whereas in middle-sized broods the relationship is significant but negative (Spearman's rank correlation coefficient: small broods, $n = 36$, $\rho = 0.273$, $p = 0.0526$; medium broods, $n = 38$, $\rho = -0.333$, $p = 0.0212$; large broods, $n = 24$, $\rho = 269$, $p = 0.0895$).

Parental expenditure is predicted to increase with chick age if hens invest in accordance with offspring reproductive value, but to decline if they invest in relation to chick vulnerability (Section 5.1.4). However, the relevance of these predictions to time spent walking are difficult to quantify, since unlike vigilance and chick feeding, walking is not a behaviour pattern performed entirely by the parent on behalf of her brood; in other words, if the hen walks, her chicks walk too (and *vice versa*). The proportion of time allocated to walking may thus vary with chick age in relation to the chicks' ability to walk themselves, which will increase with chick age. This hypothesis produces identical predictions to those of investment in relation to chick reproductive value: hens with older broods should walk more than those with young broods. The rather ambiguous results obtained do not provide conclusive evidence for any of the hypotheses suggested in Section 5.1.4, although the overall significantly positive relationship obtained through multiple regression analysis (Table 5.7) suggests that chick reproductive value and/or walking ability may be important in determining the time spent walking.

The relationship between walking and brood size will depend upon the function of walking, as discussed above and in Section 5.3.1. Suggested functions include seeking other parent females to join, for the benefits of gang-brooding, or searching for food for the chicks. If hens are looking for conspecifics, time allocated to walking should be unshared - *i.e.* independent of brood size. If, however, hens are searching for chick food, we would predict that the behaviour pattern will be shared, and expenditure should increase with brood size.

Figure 5.7 and Table 5.7 show that time spent walking increases significantly with brood size, suggesting that the behaviour pattern is shared. The relationship is however confounded by chick age; although a positive relationship is maintained within each chick age category, the correlation is not significant in the youngest chick age category

(Spearman's rank correlation coefficient: young chicks, n = 28, $\rho = 0.182$, p = 0.1711; middle-aged chicks, n = 36, $\rho = 0.478$, p = 0.0021; chicks near fledging, n = 34, $\rho = 0.306$, p = 0.0367). The relationship is also affected by female age and female weight, being significant for old hens and light hens, but non-significant for young and heavy ones (Spearman's rank correlation coefficient, female age: young females, n = 23, $\rho = 0.153$, p = 0.2358; old females, n = 51, $\rho = 0.265$, p = 0.0307. Spearman's rank correlation coefficient, female weight: light females, n = 36, $\rho = 0.414$, p = 0.0071; heavy females, n = 38, $\rho = 0.067$, p = 0.3409).

Time spent walking is not significantly correlated with either group size or time in season. Season is correlated with female weight (Table 5.6), but when examined within each female weight category, there remains no significant relationship between season and walking (Spearman's rank correlation coefficient: light females, n = 36, $\rho = -0.148$, p = 0.1894; heavy females, n = 38, $\rho = -0.036$, p = 0.4129). If time spent walking is a reliable measure of parental expenditure, these results suggest either that hens are investing in accordance neither with offspring reproductive value, nor with renesting potential; alternatively, both factors could affect expenditure on walking, but in opposite directions.

5.4 Discussion and conclusions

The aim of the study described here was to investigate parental expenditure in terms of the relative time allocated to particular behaviour patterns. Analysis of the time budgets of peahens with and without chicks reveals that parent birds spend a significantly greater proportion of their time vigilant, feeding chicks and walking than non-parent females, and these three activities are therefore used as measures of parental expenditure.

There is considerable evidence that the function of vigilance in parental hens is to increase the probability of detecting potential predators of their chicks. As the chicks become less vulnerable and increasingly able to take care of themselves, the benefits of parental vigilance decline; this is equivalent to a shift in the benefit curve of Figure 5.1b from B1 to B2, and a correspondingly lower optimum level of vigilance. The observed decline in female vigilance with chick age supports this conclusion. Similarly, chicks amalgamated in gang-broods

appear to be at lower predation risk than those in solitary broods, through increased detection and dilution effects: if so, the benefits of parental vigilance should decline with group size, and optimal vigilance levels should also decrease (Figure 5.1b). The data are compatible with this prediction, since although hens in gang-broods are less vigilant, the calculated corporate vigilance of the whole group increases with group size (Figure 5.5).

If the benefits of gang-brooding, in terms of reduced individual vigilance, increase with group size, why do peahens not amalgamate into gang-broods larger than the typical two or three hens? Although the increase in corporate vigilance is theoretically predicted to level off with higher numbers of birds, this is not expected to occur until group size reaches five or so individuals (Figure 5.5). Sibly (1983) demonstrated that optimal group size is unstable, since such groups will be joined by individuals from sub-optimal sized groups. However, this would have the effect of enlarging the observed gang-brood size to above the predicted optimum, rather than below.

If grouping is adaptive, there must therefore be certain constraints or costs of amalgamation which counteract the benefits gained from grouping. It was suggested in Section 5.1.2 that such costs might include increased aggression, conspicuousness to predators, transmission of diseases or competition for food in larger flocks. However, time spent feeding chicks is independent of group size, suggesting that inter-brood competition may not be an important factor influencing group size. The other factors have not been investigated in the current study, but looking at the effect of group size on intraspecific aggression in the breeding season, for example, could provide an insight into how group size is determined. Additional costs could include the increased chance of adopting alien young, and this hypothesis will be discussed further in Chapter Six. Similarly, identification of the relatedness of gang-brood members (*e.g.* though DNA fingerprinting analysis) would indicate whether kin selection may play a role in gang-brood formation.

The hypothesis that parental vigilance functions as an anti-predator behaviour pattern is supported by its relationship with brood size. Predators of precocial chicks usually take single young, and vigilance as an anti-predation behaviour pattern in precocial species should be unshared, and thus independent of brood size (Lazarus & Inglis 1986). The

observations support this conclusion on the whole, although heavy females display increased vigilance with brood size. It is possible to suggest a number of explanations for this apparent anomaly (*e.g.* heavy hens are not so constrained by the need to eat as light hens, and therefore invest more in larger broods simply because they are of higher reproductive value), but it is also important to bear in mind that both parametric and non-parametric analyses found brood size to have no influence on vigilance. In order to avoid the risk of committing a Type I error (see Section 5.3.1), such unexpected correlations should be treated with caution.

The proportion of time allocated to feeding chicks declines with chick age, which supports the hypothesis that expenditure is related to the chick's ability to care for itself, rather than to chick reproductive value. Parental expenditure on walking initially appears to contradict this finding, since hens with older chicks walk more than those with young broods; however, this result can be interpreted not only as an increase in expenditure with chick reproductive value, but also as investment in relation to the chick's own ability to walk. This highlights a problem of using time spent walking as a measure of parental expenditure, since it reflects not only how far the hen will walk, but also how far her brood is able to walk.

Parental expenditure on chick feeding is significantly correlated with brood size, and thus supports Lazarus & Inglis' (1986) predictions for shared investment. However, this relationship is significant only for newly hatched chicks, and may therefore reflect the development of the chicks' own ability to find food. When peachicks are very young, they may be unable to feed themselves, and rely on their mother to find food for them and hold it for them to peck at. A parent would need to spend longer finding food for a large brood than a small one. As they grow older, chicks begin to find their own food, and perhaps need the hen only to "point out" food rich areas to them, and "feeding chicks" thus moves along the scale from shared to unshared investment.

Time spent walking is significantly correlated with brood size, which is compatible with the hypothesis that the behaviour pattern is shared, and hens may be searching for food for their brood. However, this relationship does not hold in the youngest chick age category, which is in direct contrast with the conclusion discussed above, that feeding chicks is related to

brood size only in newly hatched chicks. Once again, the increasing ability of the chicks to walk confounds predictions about parental investment in walking. If very young chicks are unable to walk far, a parent hen may not allocate much time to walking, irrespective of brood size. As the chicks grow, not only do they become able to walk further, but they also require more food; this may provide one explanation of why walking is related to brood size only in the two older chick categories.

Neither female age nor female weight appear to have a significant effect on any of the three parental behaviour patterns measured. This would suggest that peahens are not investing in relation to their own residual reproductive value, or to constraints imposed by their body condition. There is however a tendency for older hens to display greater vigilance than young hens, which would lend support to the reproductive value hypothesis, but the relationship is significant only for those hens with broods of three or four chicks. I suggest that since this correlation is only just significant ($p = 0.0473$), there is little reason overall to reject the null hypotheses. Similarly, female weight is significantly (negatively) correlated with time spent walking in the late season category, but the relationship in all other seasonal and brood size categories is non-significant; hence for the reasons given above, little importance is attached to this one significant result.

One of the conclusions drawn from the study of brood defence described in Chapter Four was that females do not invest in accordance with their age, since they are long-lived birds and fecundity, fertility and survivorship may not decline significantly until an individual approaches the end of its lifespan. The results found here support this conclusion, but again it would be useful to measure behavioural expenditure by peahens throughout their lifespan.

In contrast with the findings presented here, it was reported in Chapter Four that expenditure on brood defence appears to be constrained by female body condition: heavy hens are significantly more defensive than light hens. Similar results were obtained from Chapter Three, which showed that heavy females invest more in nesting. However, both the manufacture of eggs and active defence of broods are actually or potentially high cost forms of parental investment, whereas the behaviour patterns measured in this chapter (scanning, feeding chicks and walking) may be relatively less costly. Such lower cost activities may

therefore not be physiologically constrained, resulting in no significant overall relationship between female weight and behavioural investment.

The three measures of behavioural expenditure differ in their relationships with time in the breeding season. Both feeding chicks and walking display no significant correlation with season (time spent feeding chicks increases slightly over the season, but walking declines), suggesting that neither chick reproductive value nor renesting potential individually affect expenditure; alternatively, that both factors are influential but in opposing directions. No definitive conclusions can be drawn from these results, without being able to separate the effects of renesting potential and chick reproductive value.

In contrast, vigilance displays a significant increase over the breeding season, suggesting that renesting potential may influence levels of expenditure on scanning rather than offspring reproductive value, although the relationship is not significant within heavy hens. It is possible that female weight may be a constraining factor on the female's renesting potential; heavy females have a greater chance of renesting successfully in that breeding season than light hens, and expenditure therefore increases less dramatically for heavy hens. An alternative explanation might be that chick predation pressure increases over the breeding season, perhaps as vegetation becomes more sparse, and if heavy females are better able to defend their broods than light females (see Chapter Four), they may display a less significant increase in vigilance over the season.

Conclusions

One of the most important functions of vigilant behaviour in peahens appears to be to increase the probability of detecting chick predators. This is supported by the fact that females with young chicks are more vigilant than those with older broods, and that vigilance is not correlated with brood size, since predators at Whipsnade typically take single chicks. Individual vigilance levels also decline with group size, although corporate vigilance increases, indicating that reduced individual vigilance may be one of the advantages of gang-brooding. Several costs of joining groups are suggested to account for the observed average gang-brood size being smaller than the optimum predicted from vigilance levels.

Parental expenditure in vigilance, feeding chicks and walking is not correlated with either female weight or age, suggesting that females are investing in relation neither to female residual reproductive value nor to body condition. It is proposed that the behavioural measures of expenditure used in this study may be relatively less costly than investment in nesting or brood defence; and female weight, for example, may be less of a constraining factor here than for those higher cost forms of investment.

Few of the relationships studied provide evidence for the hypothesis that peahens are investing in relation to offspring reproductive value. For example, vigilance increases over the breeding season, suggesting that renesting potential may be influential, whereas both feeding chicks and walking do not change in relation to season. Similarly, expenditure on feeding chicks and vigilance declines with chick age, in contrast with reproductive value theory; although walking does increase with chick age, this does not provide exclusive evidence of investment in accordance with chick value. In fact, the relationships of all three behaviour patterns with chick age can be attributed to the chick's increasing ability to care for itself.

Anti-predator vigilant behaviour is predicted to be unshared, and independent of brood size, in cases where single chicks are taken; feeding chicks is predicted to be shared, and increase with brood size. Both hypotheses are supported by the data. Time spent walking shows a positive relationship with brood size, suggesting that it may be a shared form of investment, such as searching for food for the chicks. However, the results are confounded by chick age, and it is concluded that the use of time spent walking as a measure of expenditure poses many problems, since the behaviour pattern is controlled not only by the hen but also by the chicks' ability to walk.

CHAPTER SIX
POST-HATCH BROOD AMALGAMATION

6.1 Introduction

6.1.1 Post-hatch brood amalgamation and alloparental care

Alloparental care is defined as care provided for conspecific young by an individual other than the genetic parent (Wilson 1975). Reports of this intriguing phenomenon are widespread in the literature, but for many years it was regarded merely as a reproductive anomaly and therefore of only anecdotal importance. In recent years however the area has received increasing attention, and has been the subject of several studies generating a number of hypotheses which attempt to explain the evolution of alloparenting behaviour (*e.g.* Gorman & Milne 1972; Williams 1974; Munro & Bédard 1977a,b; Charnov 1981; Riedman 1982; Eadie *et al.* 1988; Boos *et al.* 1989; Sherley 1990a,b). This chapter aims to investigate the causes and functions of such behaviour patterns displayed by peahens at Whipsnade.

Alloparental care was originally believed to present a puzzling example of altruistic behaviour, seemingly inconsistent with classical evolutionary theory. An altruistic act is defined as one that increases the individual fitness of the recipient of the act, at some cost to the individual fitness of the benefactor (Hamilton 1964). Since evolutionary theory predicts that natural selection will operate to maximise an animal's own fitness, alloparental behaviour is apparently maladaptive; why should an individual invest its resources in promoting the survival of another's offspring, expending energy that could otherwise be devoted to its own young?

According to Riedman's (1982) review of the evolution of alloparental care and adoption, the phenomenon has been reported in over 150 species of birds and 120 species of mammals. It would seem unlikely that an entirely maladaptive behaviour pattern could be so

widespread and persistent, and further investigation shows that in certain situations it is possible for alloparental care to have evolved as an adaptive strategy. In these cases such behaviour will increase the individual and/or inclusive fitness of the genetic parent and/or the alloparent (Riedman 1982; Andersson 1984).

In their comprehensive review of the phenomenon in North American waterfowl, Eadie *et al.* (1988) have provided a useful framework of alternative hypotheses for the evolution of alloparental behaviour, although they reject many of the "value-ridden" labels that have been attached to forms of alloparental care by previous authors (*e.g.* Riedman 1982). They favour instead the "neutral" terms *pre-hatch* and *post-hatch brood amalgamation*, which imply nothing about the the adaptive value of the observed behaviour. Pre-hatch brood amalgamation (pre-HBA), which includes behaviour patterns that other authors have termed *brood parasitism*, *nest parasitism* and *dump-nesting*, has been discussed in more detail in Section 3.4.

Post-hatch brood amalgamation (post-HBA) occurs when a female (or mated pair) incubates and hatches her own young, but the young mix with the brood of another female after hatching (Eadie *et al.* 1988). In many ways the selective processes governing the development of post-HBA are the same as those shaping pre-HBA: both involve the transfer of the care of an offspring from its parent, the donor, to another individual, the recipient, whether or not either are knowing or willing participants in the exchange. Proximate mechanisms may differ, but adaptive explanations are likely to be similar (Eadie *et al.* 1988).

As with pre-HBA, the lack of stringent definitions of post-hatch behaviour patterns has led to a variety of overlapping and confusing terms. For example, the definition and function of the term "crèche" differs widely between authors: it has been used to imply the acceptance of alien young into a brood (*e.g.* Williams 1974), the huddling together of chicks for warmth or protection, without guardians (*e.g.* Davis 1982a; Evans 1984a,b; Carter & Hobson 1988), the grouping of several adults and broods (*e.g.* Boos *et al.* 1989), or the amalgamation of large numbers of young, tended by a few adult guardians (*e.g.* Berry 1972; Gorman & Milne 1972; Munro & Bédard 1977a; Bertram 1979; Sprunt 1988).

Eadie *et al.* (1988) have resisted the use of specific terms describing particular types of amalgamation behaviour, preferring instead to encompass them in the broad category of post-HBA. Nevertheless, I believe it would be useful to identify the various components of post-HBA, provided the terms have strict and mutually exclusive definitions and are used simply in a descriptive sense, with no adaptive value attached to them. Four categories of post-HBA can thus be identified: crèching, gang-brooding, adoption, and kidnapping. All may occur on a temporary or permanent basis, apart from adoption, which implies a long-term transfer of care.

Definitions

The term *crèche* was defined by Munro (1975) as "a group containing any number of adult female(s) and [young], two or more of which are parentally unrelated". The adults attending a crèche are not necessarily the parents of any young within the crèche (Patterson *et al.* 1982; Schmutz *et al.* 1982; Kehoe 1986). The phenomenon is particularly common among the Anatidae (*e.g.* Munro & Bédard 1977a,b) and the Phoenicopteridae (*e.g.* Sprunt 1988).

The phrase *gang-brooding* was first used by Warhurst & Bookhout (1983) in their study of the Canada goose *Branta canadensis*, to describe "an aggregation of goslings from at least two broods that travel, feed, and loaf together while accompanied by one or more breeding adults and sometimes subadults". This definition is thus directly applicable to similar behaviour observed in other social bird species, and could even be extended to encompass other orders displaying this type of communal rearing, such as the social canids (*e.g.* Gittleman 1985).

The term *adoption* refers to cases in which a single female or mated pair accepts foster young as one of their own, as demonstrated by birds adopting alien chicks into their own brood, or seals caring for orphaned pups (*e.g.* Abraham 1978; Graves & Whiten 1980; Holley 1981; Riedman & Le Boeuf 1982; Hébert 1988; Plissner & Gowaty 1988; Boness 1990).

Kidnapping is defined as a situation where a female (or pair) actively kidnaps the offspring of another, and takes charge of the young for their own (apparent) benefit. Examples include the Canada goose (Nastase 1983), many primates (*e.g.* Deag & Crook 1971; Hrdy

1976; Packer 1980), and several species of fish (*e.g.* McKaye & McKaye 1977; Sargent 1989).

The four categories described above can be combined into two main types, with similar cost/benefit trade-offs predicted for each type. Crèching and gang-brooding both involve the amalgamation of chicks from two or more broods into larger groups, which may be attended either by one or both parents of each brood (gang-brooding), or by any number of related and/or unrelated adults (crèching). Adoption and kidnapping imply the transfer of the care of one or more chicks from their natural parent to another adult, and generally involve fewer individuals than either crèching or gang-brooding. The two main categories will be considered in Sections 6.1.2 and 6.1.3, and the related phenomena in peafowl are discussed in Section 6.2.

6.1.2 Crèching and gang-brooding

The grouping together of large numbers of chicks has been observed in several taxonomically diverse families, including penguins, pelicans, flamingoes, seabirds and many species of waterfowl (*e.g.* Stonehouse 1953, 1960; Evans 1984a,b; Sprunt 1988). The phenomenon may represent a behaviour pattern essential for chick survival, at a time when the young are most vulnerable; an opportunistic strategy (for any party involved); or it could be the result of incidental clustering around some resource.

The major adaptive functions of post-HBA thus appear to be (a) thermoregulation, (b) food exploitation, and (c) protection against predators (see *e.g.* Davis 1982a). An alternative explanation (d) is that the behaviour pattern is a response to ecological constraints; for example, in situations where parents are forced to forage away from the breeding site, brood amalgamation may have evolved as a substitute for parental care (*e.g.* Gorman & Milne 1972; Evans 1984a,b). Studies of crèching and gang-brooding in a range of species have provided evidence which can be used, directly or indirectly, to test the above hypotheses.

(a) Thermoregulation

If the main function of post-HBA in a particular species or population is thermoregulation, one predicts that crèching should occur when air temperatures are low, and crèched young should display increased body temperatures and/or lower metabolic rates (Evans 1984a,b).

The crèching of chicks is vital for chick survival in several Antarctic species of penguin (*e.g.* Roberts 1940; Stonehouse 1953, 1960; Sladen 1958; Carrick 1964; Davis 1982a,b). Chicks huddle together without adult "guardians" while their parents are foraging for them at sea, and parents return at intervals to feed their own young. Chick recognition in penguins may be primarily via visual cues (Sladen 1958) or vocalisations (Stonehouse 1960), or a combination of the two, and in the more territorial species it may involve site recognition (Richdale 1957).

Similar crèching behaviour, or "pod" formation, has been described in several ground-nesting pelicans (*e.g.* McGillivray 1923; Behle 1958; Bent 1964; Schaller 1964; Brown & Urban 1969; Vestjens 1977; Crivelli 1981; Evans 1984a,b) and a number of seabirds, including several gulls, terns and cormorants (see reviews in Evans 1980a, 1984a; Davis 1982a; Carter & Hobson 1988). Brood amalgamation in these families appears to be, at least in part, an adaptive response to low temperatures in the absence of parental brooding, although in some species clustering may be accentuated in the presence of danger, thereby affording protection against predation during the most vulnerable period of chick development (Stonehouse 1953; Sladen 1958; Schaller 1964; Davis 1982a; Evans 1984a,b; Carter & Hobson 1988).

(b) Exploitation of resources

One of the hypotheses suggested for the function of grouping in adults is more efficient food exploitation (e.g. Krebs & Davies 1987), and it is possible that brood amalgamation could serve a similar purpose for the young. If chicks benefit from gang-brooding in this manner, one predicts that young in groups should feed or be fed more than chicks in solitary broods.

Adults can benefit from grouping in several ways; for example, by finding spatially or temporally unpredictable food more rapidly (*e.g.* Krebs *et al.* 1972), by information sharing (*e.g.* de Groot 1980; but see Bayer 1982), by flushing prey from hiding places (*e.g.* Morse 1970), or by cooperating in the pursuit of prey or the defence of a discovered or captured food source (*e.g.* Schaller 1972) (for a review, see Pulliam & Caraco 1984). There appear to be few studies of improvements in food exploitation by young in groups, although many carnivores hunt cooperatively to provide meat for the cubs (*e.g.* McFarland 1981), and Brown *et al.* (1978) found in communally breeding babblers that the *per capita* foraging effort on behalf of nestlings increases as the number of helpers in a group increases.

(c) Protection against predators

If the function of crèching or gang-brooding is anti-predation, we would expect amalgamation to occur while the young are still vulnerable, and the presence of a predator may increase the tendency to amalgamate.

The chicks of several flamingo species form vast "nurseries" of up to 30,000 young, which are accompanied by a few adult nursemaids (Brown 1958; Rooth 1965; Kahl 1970; Brown & Root 1971; Berry 1972; Sprunt 1988; Perrins 1990). It has been suggested that in these species the adult feeding grounds are too far from the nesting areas for the young chicks to travel easily, so the young are left in the crèches while their parents collect food (Kahl 1970; Berry 1972). Parents feed their own chicks, and recognition occurs predominantly through vocal cues (Sprunt 1988). Since flamingoes are rarely subjected to low temperatures, and crèches form while the chicks are young and vulnerable, chicks apparently join together in such large numbers in order to benefit from a reduction in predation risk.

There is also evidence in some species of waterfowl that crèching enhances offspring survival, and is more likely in the presence of predators (*e.g.* Munro & Bédard 1977b; Kehoe 1986, 1989). Explanations include that a tightly-packed group may be easier to defend (Gross 1938; Lack 1947); there may be safety in numbers, through either the "selfish herd" effect (Hamilton 1971; Nastase 1983) or simple prey dilution (Munro & Bédard

1977b; Eadie & Lumsden 1985; Eadie *et al.* 1988; Boos *et al.* 1989); or the presence of more pairs of eyes may provide greater protection against aerial predators (Kear 1970).

(d) Accidental amalgamation

Brood amalgamation is not necessarily an adaptive strategy, but may be a response to ecological constraints. If post-HBA is the result of accidental amalgamation of broods around some resource, then such crèches should occur only at those sites and broods should not travel together.

Precocial young such as ducklings and goslings do not generally form tightly packed huddles, and it is therefore unlikely that brood amalgamation could serve any useful thermoregulatory function in these species (Gorman & Milne 1972; Williams 1974). Although the strategy has been shown to increase offspring survival in several waterfowl species (see above), a number of studies have described populations in which crowding in nesting or feeding areas leads to accidental amalgamation of the young (*e.g.* Beard 1964; Williams 1974; Munro & Bédard 1977a,b; Patterson *et al.* 1982; Warhurst & Bookhout 1983; but see Gorman & Milne 1972), and the nidifugous mode of development of waterfowl species may predispose them to display this type of brood amalgamation (Eadie *et al.* 1988). Munro & Bédard (1977a) concluded that "the contingent stabilization of [common eider] groups formed following encounters (be these due to predation, chance, or alarm) seems to be a fortuitous consequence of overcrowding at the precise period when family links tend to crystallize". An alternative explanation is given by Hori (1964), who observed adult shelduck *Tadorna tadorna* attacking their broods, and suggested that crèches were the result of parental rejection of their ducklings in preparation for migration.

The examples described above demonstrate that chicks can amalgamate for a variety of reasons, whether adaptive or accidental. Much of the work on crèching and gang-brooding in birds was done more than fifteen years ago, and often no distinction is made between the proximate and ultimate causes of brood amalgamation. Proximate mechanisms of crèching could include, for example, social attraction between chicks (*e.g.* Williams 1974; Carter & Hobson 1988), or a high brood density on feeding or nesting areas (*e.g.* Munro & Bédard

1977a,b; Patterson *et al.* 1982); whereas ultimate causes would include increased chick survival through thermoregulation (*e.g.* Sladen 1958; Evans 1984a) or reduced predation risk (*e.g.* Munro & Bédard 1977a,b; Sprunt 1988). Further studies are therefore needed to clarify which of the hypotheses about the ultimate causes of post-HBA might be applicable to particular species.

6.1.3 Adoption and kidnapping

As previously discussed, both adoption and kidnapping behaviour involve the total assumption of responsibility for an alien young. Although they may therefore be regarded as rather similar forms of post-HBA, there are certain implicit differences between the strategies: kidnapping suggests an active decision to care for another's offspring, and thus implies that the alloparent gains some benefit from doing so, whereas an adopting individual may be a willing, unwilling, or even unwitting recipient of alien young. The "adaptiveness" of either strategy will depend on the cost/benefit trade-off for the individuals involved.

Most previous treatments of alloparental care (*e.g.* Riedman 1982) have considered the phenomenon from the point of view of the recipient, since it appears intuitively maladaptive for an individual to care for unrelated young. However, it may be even more maladaptive for a parent to invest in the production of an offspring, and then abandon it to the care of another individual, since the parent cannot normally be certain that its offspring will be adequately cared for. Conversely, the behaviour pattern may be an adaptive strategy, conferring some advantage to either or both parties.

The following section presents several hypotheses regarding possible selective costs and benefits associated with alloparental care, and discusses how such behaviour may have evolved through various environmental constraints, selective advantages, or even reproductive error. The behaviour pattern is considered from the perspectives of both the donor and the recipient.

1. The donor: Why should an individual entrust the care of its offspring to another?

(a) Adaptive strategy

A parent may be able to gain higher reproductive success if it can induce another individual to take over the care of its young, thereby allowing the donor more time and/or resources to allocate to the production and care of additional offspring. This behaviour pattern is strikingly similar to the pre-HBA strategy of nest parasitism (Section 3.4.2); both exploit another individual's parental expenditure. In common with nest parasitism, individuals may adopt this strategy exclusively (*i.e.* there will be specialist "brood parasites" in the population), or they may be parasitic in addition to raising their own broods (Eadie *et al.* 1988).

This alternative reproductive strategy may be regarded as a "mixed ESS" (Maynard Smith 1982), occurring when the fitness of the donor is initially higher than that of the recipient; the frequency of brood parasites in the population will continue to increase until the fitness of the two strategies stabilises at equality (Andersson 1984). However, such a deliberate "policy of abandonment" runs the risk that the chick(s) will be rejected by the host, thereby decreasing the donor's reproductive success to below its potential, had it raised the offspring itself.

(b) Constraints

If it is impossible or uneconomic for a parent to raise its brood to independence, for example through physiological or ecological constraints, it may be "forced" to leave the care of its offspring to another individual in order to achieve any reproductive success at all from that breeding attempt (Lack 1968; Kear 1970; Eadie *et al.* 1988). Such constraints can be divided into three categories:

(i) Body condition and energy resources. A female bird, for example, might have the resources available for egg production and incubation, but be in too poor a condition to care for the chicks until independence. Brood desertion could increase her lifetime fitness at the

expense of a single season's reproductive effort (Ricklefs 1974). Where food resources are isolated, unpredictable, or consist of large prey, a pack-hunting or group foraging strategy may be necessary for safety or for efficient exploitation of resources, leading to communal breeding and cooperative rearing (*e.g.* van Lawick & van Lawick-Goodall 1971; Bekoff 1975; Rood 1975, 1978; Riedman 1982).

(ii) Immaturity or inexperience may have similar effects to those of depleted reserves, *i.e.* a young or novice female may be unable to raise a brood beyond hatching. An inexperienced individual may also be less broody or less dominant, and hence be more susceptible to losing its brood through kidnapping (*e.g.* Nastase 1983).

(iii) Competition for brood rearing areas. Alloparental care in precocial birds can occur as an inadvertant consequence of competition, if the broods of competing individuals mingle (see also accidental amalgamation, below) (Savard 1987; Eadie *et al.* 1988). It can also be an adaptive strategy, resulting from competition between individuals for limited brood feeding territories; a losing individual may gain more from leaving its brood with a successful individual, since it would be unable to find sufficient food for its young itself (see *e.g.* Williams 1974; Warhurst & Bookhout 1983).

Breeding habitat saturation can also lead to communal or cooperative breeding, such as demonstrated by some bats (*e.g.* Davis *et al.* 1962; Brosset 1962; Gustin & McCrackin 1987) and several colonial bird species. Examples include the Florida scrub jay *Aphelocoma coerulescens* and the white-fronted bee eater *Merops bullockoides*, in which novice breeders are unable to compete with older, more experienced individuals for mates, territories or nest sites; consequently they temporarily become an alloparent, usually assisting their parents in rearing a subsequent brood(s) (Woolfenden 1976; Emlen 1978, 1981, 1992). Such alloparenting is not necessarily solely the result of nest site shortages, however, since "helpers at the nest" may benefit through kin selection, gaining parental experience, or the eventual opportunity to acquire the nesting territory (Emlen 1992).

(c) Accidental amalgamation

Adoptions can result from the accidental mixing of broods, occurring where brood density is high and at a time before the parent-offspring bond is fully developed (*e.g.* Williams 1974; Munro & Bédard 1977a,b; Patterson *et al.* 1982). If crèches are formed and subsequently separate into their constituent broods, there may be a permanent exchange of offspring if parents are unable to discriminate against alien young (see Section 6.1.2).

2. The recipient: Why should an individual provide parental care towards an alien young?

(a) Adaptive strategy

This particular aspect of alloparental care has tended to receive the most attention in previous studies (*e.g.* Riedman 1982), and there are a number of ways in which the acceptance of additional young can enhance rather than reduce the recipient's fitness:

(i) Acquisition of parental experience. This strategy will be particularly important in species exhibiting K-selected reproductive traits: *i.e.* (a) a prolonged or energy intensive period of parental investment; (b) production of single young; and (c) limited lifetime reproductive potential. In these K-selected species, the cost of providing inadequate parental care through inexperience is very high, and an important way in which a young individual can minimise these costly "mistakes" is to gain experience of parenting during its first breeding season (Emlen 1978).

Evidence in support of this hypothesis would include an increase in parental skills and reproductive success with age or experience (Lack 1966; Skutch 1976; Emlen 1978), and a high proportion of alloparents being young and inexperienced (Hrdy 1976, 1977). Many studies have provided evidence in support of either or both of these predictions (*e.g.* Coulson 1966; Raveling 1981; Baillie & Milne 1982; Afton 1984; Reiter & Le Boeuf 1991; Emlen 1992). The effects of breeding experience should however be interpreted with caution, since they can be confounded by factors such as the greater development of self-maintenance skills with age, allowing more time for breeding (Schüz, cited in Lack 1966;

Newton *et al.* 1981; Curio 1983); an increase in parenting ability with size, which is often correlated with age (Ralls 1976); and increasing investment with declining residual reproductive value (Williams 1966b; Pugesek 1981).

(ii) Exploitation. Apparent alloparental care may be the result of an individual deriving certain proximate benefit(s) from caring for another's young. The welfare of the fostered young is not necessarily of major concern, and in this sense the fostered young is being "exploited" by the alloparent. Exploitative caretaking has been reported mainly in primates (Riedman 1982), in which low-ranking individuals may temporarily gain increased social status, protection from more dominant animals, or certain reproductive advantages (*e.g.* Itani 1959; Kummer 1968; Wooldridge 1969; Deag & Crook 1971; Hrdy 1976; Packer 1980).

Exploitation and kidnapping in other orders (*e.g.* birds and fish) exists predominantly as a strategy against predation, through prey dilution, confusion, or the selfish herd effect (Humphries & Driver 1967; Hamilton 1971; McKaye & McKaye 1977; Sargent 1989). For example, Nastase (1983) showed that Canada goose *Branta canadensis* young are able to respond to their mother's alarm calls more rapidly than adopted goslings, thus leaving the latter in a more scattered and vulnerable position. Additional benefits of adoption include enhanced dominance status through having a larger brood (*e.g.* Raveling 1970; Black & Owen 1989a), faster growth rates of young in larger broods (Cooch *et al.* 1991), and a greater contribution towards vigilance (Black & Owen 1989b; Williams 1994).

(iii) Kin selection. In societies where there is a high degree of kinship, alloparenting can contribute towards an animal's inclusive fitness. According to Hamilton's (1964) rule, individuals can increase their fitness by investing not only in their own offspring, but also in the offspring of their relatives (West-Eberhard 1975). The level of investment should correlate with the degree of relatedness between the donor and the recipient. Consequently in situations where it would be impossible or uneconomic for an individual to make its own breeding attempt, it can still increase its inclusive fitness by investing in the offspring of close relatives (Brown 1978; Emlen 1978, 1981; Brown *et al.* 1982; Reyer & Westerterp 1985; Smith 1990). Fostering behaviour is particularly prevalent in species with male

dispersal and small, closed matrifocal groups (*e.g.* lions *Panthera leo*, Carr 1965; Schaller 1972; Bertram 1976).

(iv) Reciprocal altruism. Alloparental care may be profitable if there is a high probability of receiving some future return on the investment; *i.e.* the act is one of reciprocal altruism (Trivers 1971). Perhaps the only clear example of reciprocal cooperation is that of "babysitting" behaviour, whereby a female with young can gain increased foraging freedom by leaving her offspring with another individual, which may be kin or non-kin (West-Eberhard 1975; Riedman 1982). The strategy has been widely reported in primates and cetaceans (*e.g.* Tavolga & Essapian 1957; Lancaster 1971; Hrdy 1977; McKenna 1981), but I know of no incidences of babysitting behaviour in birds.

(b) No costs, no benefits

There may be situations in which alloparenting has no significant effect on the reproductive success of the recipient. In birds, such cases are more likely to occur in precocial than altricial species, since the former invest relatively less in post-hatch care and the cost of raising additional young may be small (Nudds 1980; Andersson 1984; Eadie *et al.* 1988). It is extremely difficult to prove experimentally that the fitness costs of adoption are indeed negligible, but a few studies have shown comparable survival and fledging success of precocial broods with and without extra adopted young (*e.g.* Warhurst & Bookhout 1983).

(c) Constraints

Even when there is evidence that alloparental care does impose some fitness cost on the recipient, the recipient may be inclined to accept alien young because either (i) it is unable to distinguish unrelated young (*e.g.* Rothstein 1975a,b,c), or (ii) it is able to recognise foreign young but is unable or unwilling to discriminate against them, leaving it the alternative only of abandoning the entire brood (*e.g.* Nudds 1980).

(i) Alloparental care through the inability to recognise alien young has been termed a "misplaced reproductive function" (Williams 1966a) or "reproductive error" (Riedman 1982). That the behaviour pattern is a response to constraints rather than an adaptive

strategy is demonstrated by cases of interspecific nest parasitism, since such care cannot possibly be adaptive for the host (*e.g.* the deposition of parasitic cuckoo *Cuculus canorus* eggs in reed warbler *Acrocephalus scirpaceus* nests).

Many instances of alloparental care have been reported to occur during the initial period after birth or hatching, and have been attributed to the incomplete development of the imprinting process (*e.g.* Williams 1974; Hrdy 1976). "Imprinting" is defined as visual, vocal and/or chemical recognition, and thereby preferential attachment, between parent and young (Lorenz 1935; Hess 1973; Hess & Petrovich 1977; Gubernick 1981).

Hrdy (1976, 1977) observed that hanuman langur *Presbytis entellus* allomothers included not only young and/or inexperienced females, but also a significant proportion of pregnant females and lactating mothers, especially those who were recently parturient or had lost their infant; she suggested that these allomothers "might be hormonally 'geared' for motherhood and, hence, more motivated to adopt an orphan".

Fostering is often prevalent in other mammals, such as many pinniped species, that breed in dense colonies and in relative synchrony, and is commonly associated with females that have recently given birth or become separated from their pups (*e.g.* Fogden 1971; Riedman & Le Boeuf 1982; Boness 1990). However, Petrinovich (1974) found that female northern elephant seals *Mirounga angustirostris* are able to distinguish their own pup's distress call from those of other pups, and it appears likely therefore that the propensity for breakdown of the recognition system will depend on the density and breeding ecology of the particular population under observation.

Since the initial period post-partum is so critical for the development of the imprinting process, it may be advantageous for some group-living animals to give birth in relative solitude, in order for the recognition system to be fully operational before the individual and its young rejoin their conspecifics (Spencer-Booth 1970; Riedman 1982). It has been demonstrated in several domestic mammals (and some wild birds) that recently post-parturient and occasionally pre-parturient females accept and adopt alien young, whereas mothers with older young rarely foster aliens (*e.g.* Pilter 1954; Hafez *et al.* 1962; Hersher *et*

al. 1963; Klopfer & Klopfer 1968; Gubernick 1980). Similarly, many female artiodactyls leave the herd just prior to giving birth and may remain isolated for a short period following parturition (*e.g.* Laws & Clough 1966; Rudge 1970; Lott 1972, cited in Riedman 1982; Dagg & Foster 1976), but there are alternative explanations for this behaviour pattern, such as reducing the risk of juvenile predation (Gosling 1969).

(ii) In some cases, alloparents may be capable of recognising alien young, but the costs of rejection are higher than the costs of providing care (Eadie *et al.* 1988). As previously discussed, for some precocial birds the cost of caring for additional chicks may be negligible (see "no costs, no benefits" above), and may be lower than either (a) the energetic costs of expelling foreign chicks (*cf.* Nudds 1980), or (b) the risk of rejecting one of the alloparent's own offspring by mistake (*e.g.* Beecher 1981). Thus alloparenting can be adaptive, as long as the costs of expulsion outweigh the costs of acceptance. The following section investigates parent-offspring recognition in birds, and its implications for post-HBA.

6.1.4 Parent-offspring recognition

Individual recognition may be defined as the distinction of a particular individual from others, based on individually distinctive characters rather than on circumstantial evidence (see below) (Beecher 1981). An important example is parent-offspring recognition (POR), since individuals are "designed to reproduce themselves, not their species" (Williams 1966a,b), and one might therefore expect natural selection to favour parents that can discriminate their own young from others. Kin recognition, however, need not and should not invariably lead to kin discrimination (Byers & Bekoff 1986; Waldman 1988; Waldman *et al.* 1988; Barnard 1989); a parent is expected to show discrimination (the expression of recognition abilities) only when it gains overall benefit in terms of inclusive fitness. These costs and benefits will vary according to the particular environmental and social context (Waldman *et al.* 1988; Barnard 1989).

Waldman *et al.* (1988) distinguished two forms of kin discrimination: indirect and direct. Indirect discrimination is based upon cues obtained from the location or context; for example, a bird feeding chicks within a nest may be recognising the nest rather than the

chicks themselves. Direct discrimination involves the interaction between three elements: a *label* (the identifiable cue provided by the recognised object, such as a chick's plumage or calls); a *template* (the internal representation against which an individual compares the detected label); and a *decision rule* (the basis upon which the fit between label and template is translated into kin discrimination. This rule will be based upon the costs and benefits of discrimination, and the costs of mistaken identity, in each specific context).

POR has long been studied in a wide range of avian species, both precocial and altricial, including in particular gulls and terns (*e.g.* Evans 1970a,b, 1980b; Beer 1979) and swallows (*e.g.* Beecher 1981; Medvin & Beecher 1986), and the following general conclusions have been reached:

(a) POR is not an inevitable consequence of an extended parent-offspring relationship (*e.g.* Emlen 1941; Vehrencamp 1977).

(b) The development of POR appears to be some form of imprinting process, in which an individual's characteristics are learned during a brief sensitive period (Lorenz 1935; Hess 1959; Gottlieb 1965a,b).

(c) POR develops only very shortly before it is needed, *i.e.* at the onset of brood mobility (Davies & Carrick 1962; Evans 1970a,b; Burtt 1977; Shugart 1977; Colgan 1983). For example, recognition has developed by day five in herring gulls *Larus argentatus* (Tinbergen 1953), but not until five weeks after hatching in kittiwakes *Rissa tridactyla* (Cullen 1957); in both species the ages correspond to the initial intermingling of young. In contrast, Brooke (1978) found that Manx shearwater *Puffinus puffinus* chicks are unable to recognise parental calls at all, and do not even solicit food; he suggests that individual recognition is unnecessary since the young are completely immobile in nesting burrows, and the parents can simply locate the burrow to feed them.

Many studies of POR have concentrated on the parent's demonstration of the ability to discriminate between young (*e.g.* Burtt 1977), or occasionally *vice versa*, (*e.g.* Gottlieb 1971). Beecher (1981) however has stressed that the recognition of an individual entails two separate processes: the production of individually distinct cues by a sender, and the

perception of these cues by a receiver who then executes the recognition response (*i.e.* whether to disriminate or not) (see also Knudsen & Evans 1986; Medvin & Beecher 1986).

An individual will be selected to provide parental care if the benefit gained (assuming the offspring is its own) multiplied by the probability that the offspring is indeed its own, exceeds the cost of providing parental care (Beecher 1981). Several factors affect how confident an individual can be that a young is related, including the probability of cuckoldry, nest parasitism, brood parasitism, and brood mixing. The opportunity for caring for an unrelated young is therefore obviously much greater in highly social species than in solitary animals (see Colgan (1983) for a review). Apart from a few communally breeding species, which have complete sharing of all parental duties between adults within the colony, social species require a far more efficient kin recognition system than solitary ones if parental care is to be restricted to related young.

The probability that a parent bird can distinguish its own offspring depends on the parent's ability to recognise the chick's cues, as well as the chick's ability to provide those cues. Parental discrimination can spread in a population if genes for discrimination are passed on to the offspring (Beecher 1981). These offspring receive more care than the offspring of non-discriminating parents, since they will be fed and cared for not only by their own parents, but also by non-discriminating parents, and will consequently have enhanced prospects of survival and reproduction. Natural selection in this case is operating directly upon the parents to recognise the young, but only indirectly *vice versa*. Recognition by the young could therefore be a less sophisticated system; for example, a lost chick could just call repeatedly, and wait for its parent to recognise and retrieve it. There are however likely to be costs inherent in the inability of young to distinguish between adults, since a chick may approach a potential donor of parental care, but risks rebuff, injury or even death if that parent is able to discriminate between offspring.

Asymmetries of recognition can also operate in reverse. Such a situation could arise in species where the probability of intermingling is low, or there are clear circumstantial cues (indirect discrimination), and the evolution of a recognition system would therefore be unnecessary and costly (Medvin & Beecher 1986). In addition, if the parents have

distinctive cues that the young can recognise, the response of the chick to the adult becomes a cue for the adult as well (Heinroth 1911; Beer 1979).

Although the costs of *not* recognising alien young have been much discussed in the literature (*i.e.* a parent may expend parental effort on unrelated young), it is also important to consider costs of *having* a recognition system (other than where it is unnecessary, as mentioned above). Parents would be forced to spend time and energy assessing the identity of the young at every interaction, with some probability of error every time; a single mistake could result in the death of an offspring (Knudsen & Evans 1986). This could be far more detrimental to the parent's inclusive fitness than providing extra care for an alien young, particularly if the brood size is large. Beecher (1981) suggests that this cost may be the reason why POR typically does not develop until shortly before the offspring leave the nest. However, a lack of evidence for parental discrimination does not prove that a recognition system does not exist.

Among precocial species, such as the Indian peafowl, the interval between hatching and leaving the nest can be very short; peachicks usually remain in the nest for less than 24 hours. The gregarious nature of the species means that in order to be effective any recognition system must be rapidly instigated, before the young become mobile and start to mix with others (Colgan 1983).

Recognition in birds often occurs *via* calls (Falls 1982; Colgan 1983; Medvin & Beecher 1986). For calls to serve as individually distinct cues, there must be sufficient variation between individuals (Beecher 1981; Falls 1982; Jouventin 1982; Medvin & Beecher 1986), and the recipient must have the ability to distinguish between them. There is considerable evidence that avian POR systems rely primarily on parental recognition of chick calls; however, both call "signature" and parental discrimination are likely to vary over time, as described below.

Among many altricial species, the calls of nestlings are almost impossible to differentiate between individuals until they approach fledging, and parents will accept strange young for some time after hatching (*e.g.* shags *Phalacrocorax aristotelis*, Snow 1963; carrion crows

Corvus corone, Yom Tov 1976; and several swallow species (Burtt 1977; Beecher *et al.* 1981). More precocial species start to exhibit discrimination against alien chicks from between a couple of days post-hatching (*e.g.* crested terns *Sterna bergii*, Davies & Carrick 1962) and several weeks (*e.g.* kittiwakes *Rissa tridactyla*, Cullen 1957), depending upon nesting ecology (densely packed, ground nesting populations develop a recognition system earlier than more spaced, cliff nesting ones), as well as the degree of precocity (see Evans 1980a for a review). The behaviour of the chick towards the parent is also very important as a cue for parental recognition in the initial stages (Colgan 1983). Recognition improves over time post-hatching as the chick becomes increasingly familiar with the parent, thereby displaying behaviour patterns that the parent recognises as belonging to "own offspring"; and the chick cues themselves become increasingly distinguishable between individuals, thereby developing a "signature" (*e.g.* Burtt 1977; Beecher 1981).

6.2 Observations

6.2.1 Gang-brooding at Whipsnade

The phenomenon of post-HBA in peahens was introduced in Chapter Five. Females do not however amalgamate immediately after hatching; as outlined in Section 2.3.1, they generally make their nest in secluded areas some distance from the rest of the population, and keep their newly-hatched brood away from others for the first two or three days (Plate 6.1). Following the initial isolation period, a peahen usually takes her brood to join with other females and chicks in the more populated areas of the park (Plate 6.2). She continues to attend the brood, and does not leave her chicks solely in the care of other crèche "guardians". Brood amalgamation observed at Whipsnade thus appears to be covered by the definition of "gang-brooding" given in Section 6.1.1, rather than "crèching". In this context gang-brooding is defined as the amalgamation of two or more females and their broods for a period of more than five minutes, with the females and/or the broods no more than 10 metres apart (*cf.* Warhurst & Bookhout's (1983) definition). Hens are however frequently much closer than this, and the chicks have the opportunity to intermingle freely.

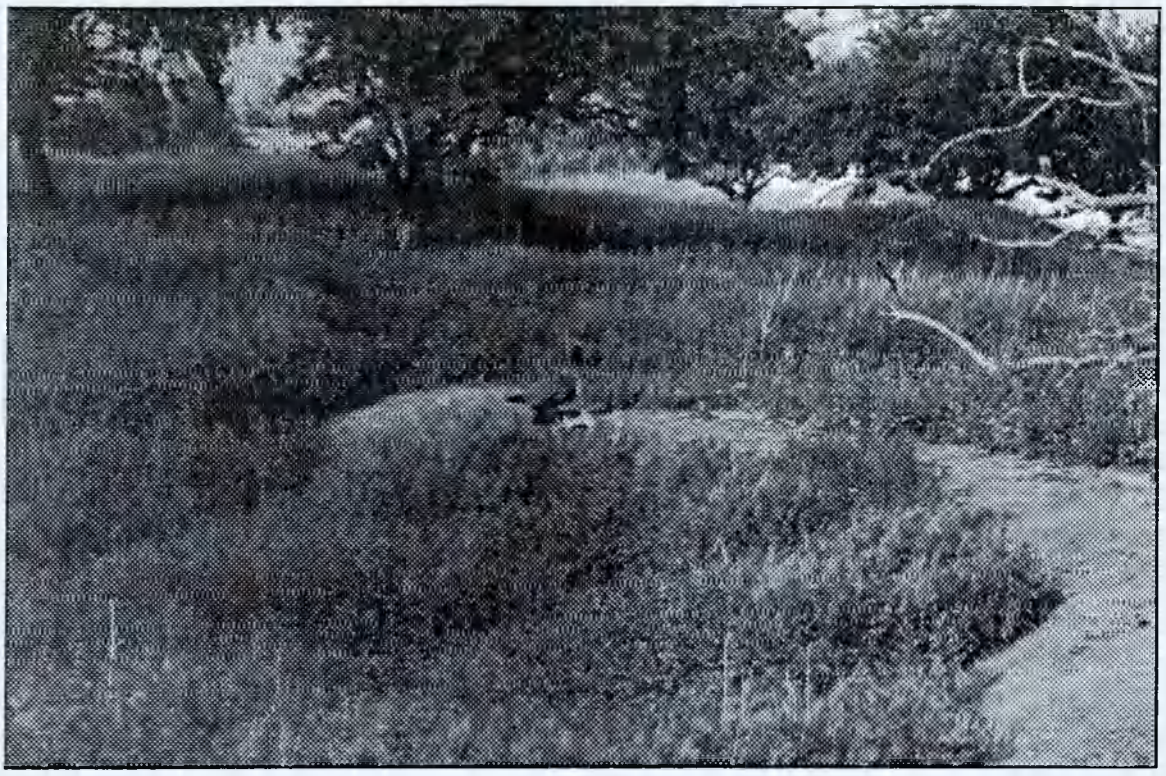


Plate 6.1. Peahen with one day old brood on Whipsnade downs.

Most gang-broods at Whipsnade consist of two or three hens with their chicks (Plate 6.2*a*), although groups of up to ten such females and broods are occasionally observed, usually clustered around feeding sites (Plate 6.2*b*). Gang-broods are not permanent, as hens join and leave them throughout the day, but may persist for up to several hours. One of the hens will then lead her brood away, thereby either dissolving the gang-brood or altering its composition. However, there appears to be relatively little variation in group membership; females are seen to amalgamate their broods repeatedly with the same hens, and these associations frequently persist between seasons, through both winter and summer months.

It is possible that the level of association between broody hens is based upon the degree of relatedness between them, and a few observations provide some support for this idea. For example, in Flint Pit Paddock in 1990 there were often around ten females with broods at any one time, three of which (A20, DBO and unringed) were leucistic. It is quite possible that these three females were related to one another, whereas they were known (from their plumage variations) to be unrelated to the other brown hens. The leucistic females were seen to gang-brood with each other more frequently than with the brown hens (Plate 6.3), which

Plate 6.2*a:* Females and their broods "gang-brooding" at Whipsnade. *b:* Five parent hens and their six chicks clustered around a feeding site; two males (and a muntjac!) also present.

may suggest some form of kin selection - for example, if the three hens were sisters, they could be cooperating to provide care for their sisters' offspring as well as their own. However, such evidence for kin selection is purely anecdotal, relying on plumage variation to give an indication of relatedness between individuals. Such genetic relationships are impossible to ascertain without detailed information from DNA fingerprinting.

Plate 6.3. Three leucistic females (A20, DBO and unringed) gang-brooding their young in Flint Pit Paddock.

Furthermore, there are alternative explanations for the behaviour; for instance, leucistic females may prefer to gang-brood with others of similar white plumage in order to reduce their own conspicuousness (and hence risk of predation) within the group; or hens of similar morphology may have similar breeding dates, and hence similarly aged young. There were also numerous occasions on which hens that were known to be unrelated amalgamated their chicks, indicating that gang-brooding is mediated by factors other than kin selection alone. This leads to the following question:

Why do peahens at Whipsnade gang-brood their young?

As outlined in Section 6.1.2, there appear to be four main routes through which brood amalgamation may have evolved, and each is considered in turn with respect to the Whipsnade population (*N.B.* the categories are in a different order, for ease of discussion).

(a) Thermoregulation

If chicks are grouped to allow the body heat of other young to act as a substitute for parental brooding, we would expect one or more of the following conditions to apply:

(i) Females attending gang-broods should not brood chicks.

(ii) Chicks should huddle closer together in severe weather.

My observations appear to rule out thermoregulation as an explanation for brood amalgamation at Whipsnade, since gang-brooding was observed throughout the entire breeding season, in all kinds of weather and at all times of day. Chicks were never seen to huddle together, so gang-brooding is unlikely to be a substitute for parental care; rather in cold or wet weather several hens may sit together, each brooding their chicks under their wings.

(b) Exploitation of resources

It was predicted in Section 6.1.2 that if chicks in gang-broods benefit from more efficient exploitation of food, then they should demonstrate higher feeding rates than chicks in solitary broods. Although no records were made of the relative feeding rates of chicks themselves in each situation, Figure 5.7 shows that the proportion of time allocated to feeding chicks is independent of group size. These observations therefore provide no support for the food-exploitation hypothesis.

(c) Accidental amalgamation

Gang-brooding behaviour may in fact not be adaptive, but could be an accidental consequence of overcrowding, or might occur because hens and broods are attracted to

common feeding sites or loafing grounds. Given that peafowl at Whipsnade have over 500 acres of available habitat, it is extremely unlikely that simple overcrowding has led to the phenomenon of gang-brooding. Thus the "accidental amalgamation" hypothesis gives rise to the following predictions:

(i) Gang-broods should occur only at known feeding sites or "loafing" grounds.

(ii) Such areas are likely to attract all peafowl, so the groups will consist of not only females and broods, but also males and non-breeding hens.

(iii) Gang-broods should break up into individual broods as soon as the parent females leave these areas, so that hens and chicks will not be seen travelling together as a group.

Observations reveal that certain feeding or "loafing" areas do attract all categories of peafowl, including males and non-breeding females (see Plate 6.1*b*). However, it is much more common to see gang-broods of two or three hens and their chicks travelling together, away from such areas, and these groups will only ever consist of females with their broods. The accidental amalgamation hypothesis therefore seems unlikely.

(d) Protection against predators

Predictions

Gang-brooding as a protection against predation may benefit chicks directly, such as through prey dilution, confusion, the selfish herd effect, or increased probability of predator detection. The behaviour pattern can also benefit the hen directly, simply through the advantages of being in a group, or by sharing the cost of caring for her brood. The hypothesis that gang-brooding has an effective anti-predation function for the chicks leads to several predictions:

(i) Gang-broods should form while the young are still vulnerable to predators.

(ii) Chicks in gang-broods should suffer a lower predation rate than chicks in single broods.

(iii) Gang-broods may form, or coagulate more closely, in the presence of a predator.

(iv) If the anti-predator benefits of gang-brooding are gained primarily by the chicks, we would expect the corporate level of vigilance in gang-broods to be higher than that of solitary hens, thus leading to a greater probability of predator detection.

(v) Gang-brooding may benefit the female directly, through a reduction in the costs of parental care. If so, we would expect each female attending a gang-brood to display higher levels of self-maintenance activities (such as eating and preening) and lower levels of anti-predation behaviour patterns (such as vigilance) than solitary hens with broods.

Observations

The predictions (i) to (v) above will be considered in turn, in relation to gang-brooding behaviour observed in the Whipsnade population.

(i) Gang-brooding can be seen throughout the entire breeding season and continues until the winter months, when the chicks are several months old and females and their offspring start to travel and forage increasingly independently. By this stage the young birds are much less susceptible to predation by small mammals (*e.g.* rats, stoats and weasels) and birds (*e.g.* crows, magpies and captive white storks), and dissolution of gang-broods coincides with a decrease in their presumed anti-predation function. However, gang-broods do not form during the first two or three days after hatching, when chicks might be considered to be at their most vulnerable.

(ii) Very few data could be gathered on the mortality rate of chicks in gang-broods compared with those in solitary broods, as very few natural attacks by a predator were ever directly observed. However, these attacks were all on chicks in solitary broods. Some attacks were by white storks *Ciconia ciconia* in Flint Pit Paddock (Plate 4.1), and on one occasion a parent female attempted successfully to defend her brood against the larger, more aggressive bird, which pecked, killed and subsequently consumed one of her three week old chicks (Plate 4.2).

In another case, two crows were seen attacking a small peachick (probably less than two weeks old) which had become slightly separated from the rest of its broodmates. This

limited circumstantial evidence may therefore point towards higher chick survival in gang-broods. However, since gang-broods could not be observed continuously, and all marked chicks were observed both in gang-broods and in solitary broods on different occasions, it was impossible to infer whether the loss of a marked chick had occurred while the individual was in a single brood or a gang-brood.

(iii) As described above, natural predator attacks on single broods or gang-broods were rarely observed, and consequently data on the responses of chicks to predators could be obtained only by experimentation. From the observations of brood defence described in Chapter Four, some qualitative behavioural data could be extracted about the responses of gang-brooded chicks to the approach of a predator.

In undisturbed gang-broods, hens normally feed, rest and travel fairly close together, their broods remaining next to them when very young but mingling increasingly with other broods in the group as the chicks grow older. When approached by the "predator", the female which initially becomes aware of the danger utters a "honk" of alarm which alerts the other hens. Each female then begins to honk and cluck loudly, with raised tail and lowered wings, appearing to muster her chicks close to her. All hens and their broods then move away from the source of danger as quickly as possible, circling as if to check that their chicks are staying close by. Thus when approached by a predator, a gang-brood does not usually cluster more tightly; instead each hen will call her brood after her and flee independently from the danger. If gang-brooding has an anti-predation benefit, it does not therefore appear to be through the selfish herd principle, for example, but rather perhaps through increased probability of detection (although the responses described in Chapter Four may be specific to the type of predator encountered).

(iv) Vigilant behaviour in parent peahens was investigated in Chapter Five, including the relationship between vigilance and gang-brooding. It was concluded that the most likely function of vigilance was to increase the probability of detecting chick predators, and evidence for this hypothesis was provided by the higher level of vigilance of hens with younger chicks, the lower individual female vigilance in groups (where broods may be

safer), and the lack of a relationship between vigilance and brood size, as predicted by Lazarus & Inglis (1986) for "fixed loss" types of predation (Figure 5.4).

(v) It was also demonstrated (Figure 5.6) that corporate vigilance (the probability that at least one adult will be vigilant at any one time) is likely to rise with gang-brood size, lending support to the idea that gang-brooding functions to reduce predation levels. Care must be taken not to invoke a circular argument with respect to vigilance and grouping ("vigilance has an anti-predation function because vigilance declines when in a group, where chicks are safer", as well as "gang-brooding has an anti-predation function, since corporate vigilance increases as group size increases"). Nevertheless, additional support for the anti-predator function of vigilance is described above, and if that hypothesis is accepted, it can be seen that gang-brooding can benefit members both by reducing individual vigilance and increasing corporate vigilance levels.

It appears thus that the phenomenon of gang-brooding in peafowl is not the result of accidental amalgamation, or for the purposes of thermoregulation or food exploitation, but its most probable primary function is seemingly associated with protection against predators. Gang-brood formation thus appears to be an adaptive strategy for peahens, maximising the efficiency of their anti-predator vigilance behaviour.

The question was raised in Section 5.4 of why, if the anti-predator benefits of gang-brooding increase with group size, peahens do not form larger groups than the usual two or three parent females observed. It was suggested that gang-brooding may incur costs as well as benefits for the parties involved, such as inter-brood aggression or competition for resources; there is also a very real danger that the intermingling of young from different broods might lead to brood-mixing, resulting in the fostering of unrelated chicks. The timing of gang-brood development, and the sizes of gang-broods observed, may therefore be the result of a trade-off between the anti-predator advantages of large groups, and the costs of aggression, competition and adoption. The phenomenon of adoption among the Whipsnade population, with suggested causes and consequences, will be discussed in Section 6.2.2, and the hypothesis that gang-brood formation may be related to the costs of adoption will be explored in Section 6.3.

6.2.2 Adoption at Whipsnade

Observations reveal that peahens are not necessarily willing recipients of alien young: on many occasions I saw females attacking such a chick which had approached too closely, even flinging it into the air. In contrast, peahens maintain vocal contact with their own brood by clucking continually, whether they are solitary or part of a gang-brood. The chicks respond with high "peeps" as they follow, and simply call more loudly if separated from the brood. This corresponds directly with Beecher's (1981) description of a situation in which chicks are selected to provide a signature, and the parents to discriminate between signatures (Section 6.1.4). A peahen who has lost her brood will call agitatedly, with very loud "honking" calls; these parent-young vocalizations can be heard from some considerable distance, and usually result in the two parties being reunited.

Nevertheless, the occurrence of adoption, in which a female was observed caring for a chick that had not hatched from her own nest, was not uncommon in the Whipsnade population; I estimate the frequency of adoption (*i.e.* the proportion of broods containing at least one alien young) to be approximately 20% of all broods. I determined instances of adoption in three ways: firstly, by individually marking females and chicks, I was able to observe transfers of young between broods; secondly, any increase in the size of a marked hen's brood, or, more rarely, discrepancies in the ages of the chicks (Plate 6.4), would indicate that she had fostered extra chick(s); and thirdly, in several cases either I was able to directly observe adoption taking place, or else there was very strong evidence that it had occurred (see the individual case histories outlined below).

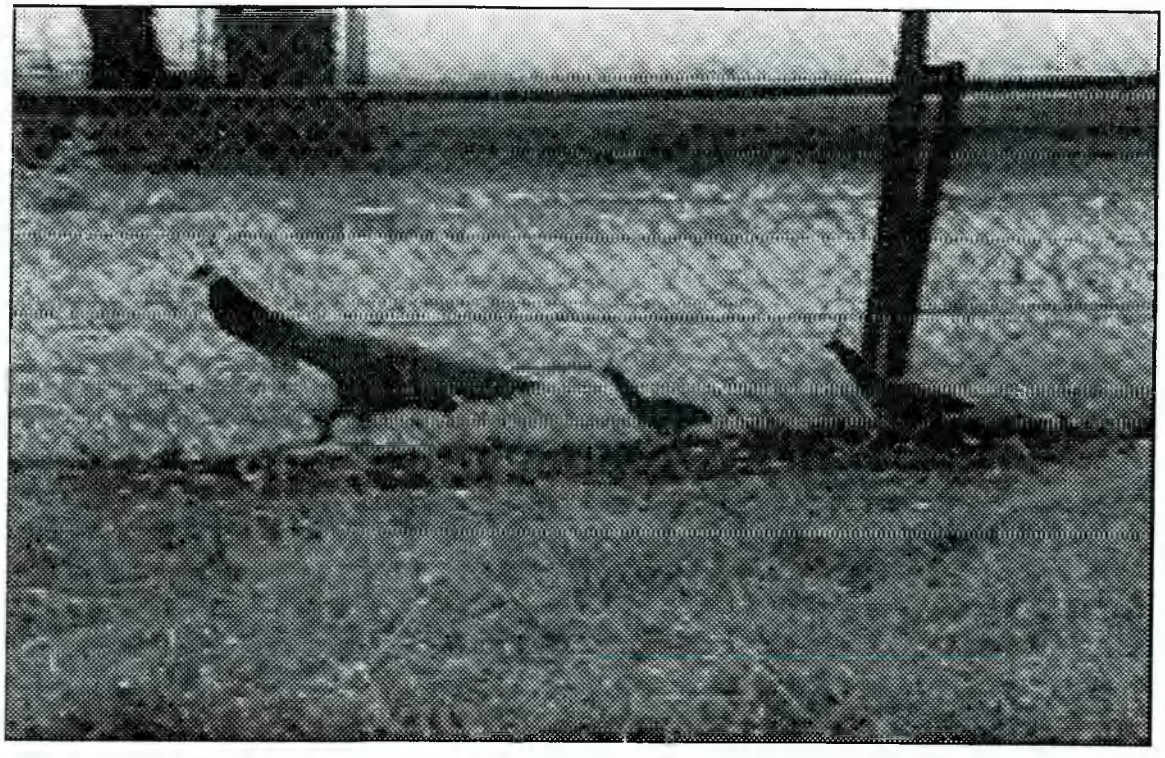


Plate 6.4. Nessie has given birth! Evidence of adoption at Whipsnade: peahen and brood containing two chicks of different sizes. The smaller chick was tagged, and evidence suggests that it belonged to this hen; the larger was unmarked, and believed to have been adopted.

Outlined below are three particular cases of adoption, which seem to be typical of fostering behaviour in the Whipsnade population.

(a) A20 (leucistic) and RG (brown); unrelated females

25th June 1400 RG hatched five brown chicks from her nest in Flint Pit Paddock.

1800 RG had five brown chicks in Flint Pit Paddock.

29th June 2000 A20 had been sitting on her clutch of seven eggs for 27 days (*N.B.* normal incubation period is 28-30 days). Her nest was 55 metres from RG's nest in Flint Pit Paddock.

30th June 0600 A20 had deserted her clutch and was brooding and defending a small brown chick.

0730 RG seen with only four brown chicks; the evidence points to A20 having adopted RG's other chick.

July onwards A20 continued to care for the brown chick throughout the season. RG raised two of her remaining chicks to independence.

(b) B45 and B39 (both brown females)

15th June 1500 B45 hatched five brown chicks from her nest by the oryx shed.

18th June 1230 B39 had three brown chicks in gazelles paddock. Chicks all had egg teeth, and must have hatched on 17th or 18th June.

20th June 1000 B39 seen in gazelles paddock; she had lost her chicks.

1500 B45 seen with four brown chicks in gazelles paddock.

28th June 0830 B39 and B45 were both in gazelles paddock. B45 had four brown chicks; B39 had none. While I was capturing B45's brood for marking, both B45 and B39 were defensive of the chicks, but all four chicks followed B45. Both hens remained calling in the paddock while the chicks were tagged; when I returned them, B45 collected all four, but as she moved out of the gazelles paddock she left one chick behind, calling loudly. B39 then became extremely broody and defensive of this chick.

30th June 1100 B39 seen in gazelles paddock, still brooding and defending the marked chick.

5th July 1200 B45 had two chicks remaining, and B39 continued to care for the other marked chick. The two broods mixed as the females foraged together, but no exchanges occurred.

(c) DBO, B27 and UL (all three leucistic hens)

June/July Females DBO, B27 and UL all had nests in Flint Pit Paddock.

5th July 1130 DBO hatched two white and one brown chick in Flint Pit Paddock.

7th July 1500 B27 hatched two brown and one white chick in Flint Pit Paddock.

8th July 1230 UL hatched two white and one brown chick in Flint Pit Paddock.

10th July 1400 DBO had two white and one brown chick, B27 had two brown chicks, and UL had two white and one brown chick, all in Flint Pit Paddock.

11th July 0800-1900 All three females tended to forage and rest together in Flint Pit Paddock, gang-brooding their chicks. Many changes were observed in the broods throughout the day; the chicks did not show any obvious concern about which female they followed, and all three females appeared to feed all eight chicks indiscriminately.

12th-15th July There was continued instability in brood membership; the three hens were seen both together and alone with brood sizes varying from zero to five.

15th July 1730 Two chicks were found dead, from predation and exposure respectively, in Flint Pit Paddock; these chicks thought to belong to UL.

16th July 1100 DBO had one brown chick (thought to be hatched from her own nest); B27 had one brown chick (thought to have hatched from UL's nest); and UL had no chicks remaining. DBO and B27 continued to care for these chicks throughout the season.

Why should adoptions occur at Whipsnade?

One might imagine that an act of adoption will probably be more beneficial for the fostered chick than for the adopting peahen, since as long as the chick is receiving adequate parental care and protection, the source of that care should make little difference to the young. Nevertheless, it is likely to be more adaptive for a chick to remain with its own family group, where it can justifiably expect to receive parental care, than to seek out a foster parent and risk being attacked. As described above, peahens were frequently seen to attack alien chicks that approached them.

A chick however should be prepared to be less discriminating, and attempt to join another brood, if its current circumstances are inadequate: if, for example, its mother is unable to find food for her offspring; or a chick is lost, when it will be without care and protection and will be very likely to perish (Evans 1970a; Beecher 1981; Falls 1982; Medvin & Beecher 1986). Such a situation could arise if a peachick becomes separated from its mother; or if a hen leaves a gang-brood without collecting her entire brood.

From the point of view of the "donating" female (*i.e.* the genetic parent of the fostered chick), it would be adaptive to give up her young only if by doing so she increases her inclusive fitness; for example, if the survival prospects of the donated chick are not markedly lowered, and the donor hen has the opportunity to divert her parental expenditure towards additional breeding attempts (*cf.* the strategy of nest parasitism discussed in Section 3.4.2).

The strategy is not so easily explained in evolutionary terms for the "recipient" female and her brood - why should she accept and invest in alien peachicks? Indeed, some hens appear to be attempting to avoid the costs of adoption by rejecting approaches from strange chicks. However, before speculating about this apparently maladaptive behaviour, it is important to determine whether these "costs of adoption" do in fact exist. Such costs might be expected to be expressed as an increase in levels of parental behaviour patterns with increasing brood size, or a decline in the benefit of a parental act accrued by each individual offspring.

Three candidates for measures of parental expenditure were isolated in Chapter Five: vigilance, feeding chicks, and walking. The last behaviour pattern can lead to some problems of interpretation, since observed variation in walking necessarily reflects not only the mother's willingness to invest in offspring, but also the chicks' own ability to walk. Nevertheless, this complication should be related only to chick age and development, and not to factors such as brood size. Vigilance levels were observed to be independent of brood size, but both feeding chicks and walking increased with brood size. There do therefore appear to be measurable costs of having a larger brood, and we may justifiably assume that the adoption of alien chicks can cost the host hen at least in terms of behavioural expenditure.

Several hypotheses for the evolution of adoption were given in Section 6.1.3. Each is considered in turn below, with respect to the behaviour observed at Whipsnade.

1. Environmental constraints: Neither food nor breeding resouces appear to be restricted at Whipsnade. Both hens and chicks eat insects and grass seeds, which are widely available throughout the Park; similarly, suitable nest sites are plentiful, and a communal breeding system is not essential for chick survival.

2. Kin selection: It is possible that some of the peahens involved in adoption are related (*e.g.* perhaps the three leucistic females described in case history (c) above; see also Plate 6.3), particularly given the matrifocal nature of juvenile dispersal, but in other cases the hens were known to be unrelated. Kin selection cannot therefore entirely explain the phenomenon of adoption at Whipsnade.

3. Reciprocal altruism ("babysitting"): there seems little opportunity for such a strategy in this population, since as adopted chick, once accepted by a foster parent, generally remains with that female for the remainder of the season. It appears extremely unlikely that the adopting hen can expect any reciprocal care of her offspring by the "donor" female.

4. Parental experience: If caring for unrelated young allows an individual to gain parenting experience prior to starting her own breeding attempt, one would expect that alloparents will be young, inexperienced females with no broods of their own. However, observations of marked hens show that many adopting females have bred previously; also that it is rare for alloparents not to already have broods of their own at the time of adoption.

5. Exploitation: I have no evidence that having a larger brood either enhances a peahen's status, or helps to dilute the effect of predation. If however adoption confers such a net advantage to the recipient female, I would not expect hens to attack alien chicks, but rather to attempt to "kidnap" them into their brood.

6. Reproductive error: If adoption is a consequence of reproductive error, it implies a failure of the recipient female to recognise and thereby discriminate against alien chicks. Since environmental constraints, reciprocal altruism, parental experience and exploitation do not appear to be responsible for the observed behaviour, and kin selection, although plausible, cannot entirely explain the strategy, the most obvious explanation is that adoption is the result of reproductive error. Several observations support this conclusion, such as the tendency for hens to initially seclude their broods after hatching, thus enabling female and offspring to imprint on one another. This hypothesis will be explored in greater depth in Section 6.3.

6.3 Experiments: vocal recognition of pea-chicks

6.3.1 Introduction

In Section 6.2.2 I described the phenomenon of adoption in the Whipsnade population, and considered a number of hypotheses regarding the evolution of this behaviour pattern. The

conclusion was reached that although kin selection may be an instrumental factor, it cannot adequately explain all the cases of alloparental care observed at Whipsnade. The most likely mechanism leading to post-HBA appears to be errors of recognition, and examination of the peahen's ability to recognise and respond to offspring is therefore essential when investigating why peahens might adopt alien young.

In order to investigate POR in peafowl, it is necessary to determine which features the chicks are using as identification cues, and how the parents recognise and respond to those cues. From my observations on the Whipsnade peafowl population, calling appears to be extremely important in maintaining the cohesion between a peahen and her brood: the female clucks continually and honks if agitated, and the young chicks cheep if more than a metre or so from their mother. This point is illustrated by many cases (a total of 35 were observed directly) in which a stray chick that had just become separated from its mother and broodmates would give loud distress calls. In all such instances the female began to call to her chick, even if out of sight, and both parties would move towards each other until they were reunited. Thus there is strong circumstantial evidence that the cues presented by chicks for identification are partly, if not entirely, vocal.

In contrast, many hens were seen to reject or even attack other stray chicks that attempted to join their brood: in this manner most females seem unwilling to provide parental care for alien young. There is some evidence that larger broods are more costly in terms of increased parental effort (see Section 6.2.2 and Figures 5.6-5.7), and so hens would be expected to avoid the costs of adopting extra chicks; however, such decisions about whether or not to care for a chick obviously rely on the ability of hens to recognise their own young, and to discriminate against non-relatives.

This chapter describes an experiment aimed at investigating the nature of offspring recognition in peahens, and to test the hypothesis that the susceptibility of a hen to becoming a foster parent depends upon her ability to recognise individual chicks, which is in turn dependent upon her breeding state. Thus the categories of subjects chosen were designed to reflect a range of different breeding states, from non-breeding females to hens with chicks,

and their response to playbacks of chick distress calls was used as an indication of their willingness to adopt.

6.3.2 Methods

Recordings used for playback

In the early part of the 1989 breeding season I made recordings of two of the chicks I had captured for marking, for use in the playback experiment. One chick was five or six days old, and the other was approximately five weeks old; they were recorded individually while held in the hand, in the open air away from other peafowl. I used a Uher reel-to-reel tape recorder and a microphone to record several minutes of each chick's distress calls, and a section containing six complete calls (approximately fifteen seconds) was then recorded repeatedly onto a separate cassette tape. Each individual call is a simple monotonal "cheep", with a cycle of about 0.4ms and duration 400ms (Figure 6.1).

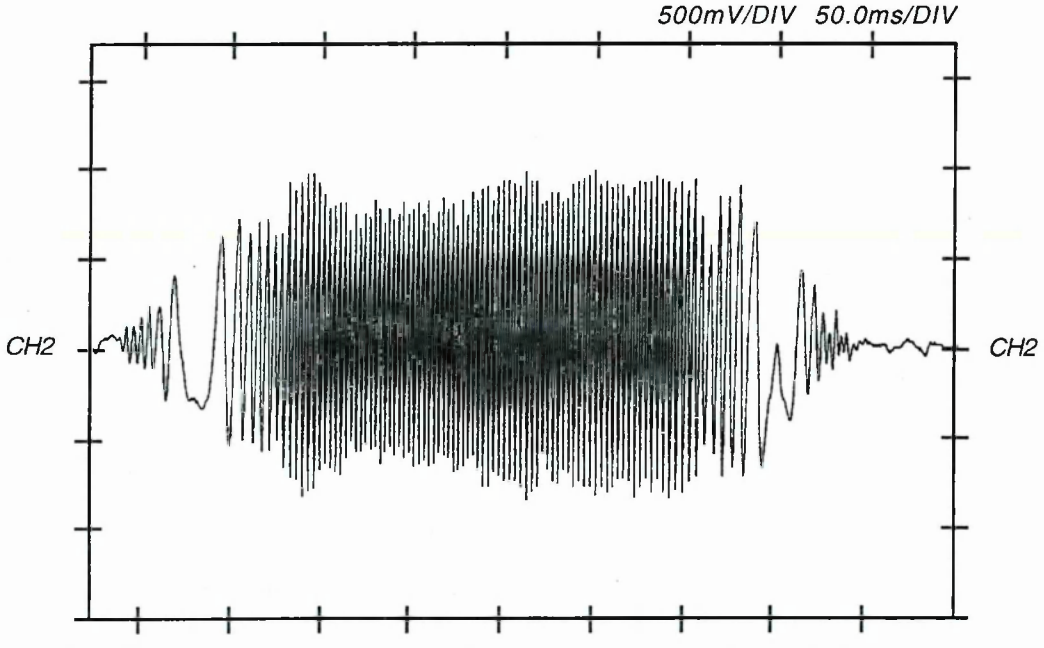


Figure 6.1. Sonogram of a single "distress cheep" of a six-day old peachick.

Two pilot studies were carried out, in 1989 and early 1990, in order to determine whether there was any differential response to the two playbacks. In each study I tested 12 hens: four incubating, four with young chicks (less than ten days) and four with older broods. I played both tape loops to each hen in random order, according to the protocol outlined in

Section 2.5.2, with at least 60 minutes between each playback. There were no significant differences in the females' responses between the two call types (Wilcoxon test, $n_1 = n_2 = 12$, $p > 0.05$) in any class of female, and so for the sake of simplicity in all subsequent playbacks I used the call of the younger chick.

Categories of females

Six classes of female subjects were designated for the playback experiment. I selected the subject categories to encompass a wide range of stages in the peahen's breeding cycle, since I aimed to discover how the responsiveness of a female might vary according to the particular reproductive stage she has reached; in other words, how she would respond to the call of an unfamiliar chick.

The six categories chosen are as follows:

(a) "Non-breeding" (**NB**): females without chicks. This category includes not only young hens, but also mature hens which may have attempted unsuccessfully to incubate a clutch or raise a brood; however, I was confident (from frequent observations) that all hens tested in this category had not been involved in nesting or brooding during the previous 20 days. The latter group, "mature non-breeders", was defined as the "control" group, and used for comparison with the other categories of hens in subsequent analysis. *(n = 31: 13 yearling females, 18 mature females)*

(b) "Early incubation" (**EI**): females sitting on the nest, within the first 15 days of incubation. *(n = 7)*

(c) "Near hatching" (**NH**): females on the nest, tested within the last three days of incubation. *(n = 11)*

(d) "Young brood" (**YB**): females with chicks less than seven days old. *(n = 16)*

(e) "Older brood" (**OB**): females with chicks older than three weeks. *(n = 13)*

(f) "Lost chick(s)" (**LC**): females which were known to have lost their brood within the five days prior to testing. This category included hens whose chicks I had temporarily removed for marking. *(n = 18)*

Experimental protocol

Subjects in categories (b) and (c) (*i.e.* on the nest) were identified prior to testing with the playback, since their location and stage of incubation were known. All other focal animals were selected according to visibility and proximity to the hide or observation vehicle at the time of experimentation. All observations were made on marked individuals, in order to avoid accidental repeated sampling.

For each playback test, I used a Sony radio/cassette player and 30 watt speaker with extension cable. The tape player was powered by eight 1.5 volt batteries, which were recharged between each experiment. The tape was operated from inside the hide or vehicle, and the loudspeaker was hidden several metres away in vegetation. The equipment was set up at least 60 minutes before each experiment, and I was in place 30 minutes before.

A minute by minute time budget of each focal female was recorded for 15-20 minutes prior to the playback, following the procedure described in Chapters Three and Five. The tape of the repeated chick call was then played for one minute, at a volume as close as possible to that of live peachicks (as perceived by the human ear). The behaviour of the focal hen was recorded at five second intervals throughout that minute, and for the following five minutes. The playback was then repeated for a further minute, and observations continued for the next five minutes. The procedure is represented diagrammatically in Figure 6.2.

The time budgets of all females in the first 15 minute sampling period (A) did not differ significantly from those expected (from the results obtained in Chapter Five), and I therefore judged that the presence of the equipment was not interfering significantly with the peahens' behaviour.

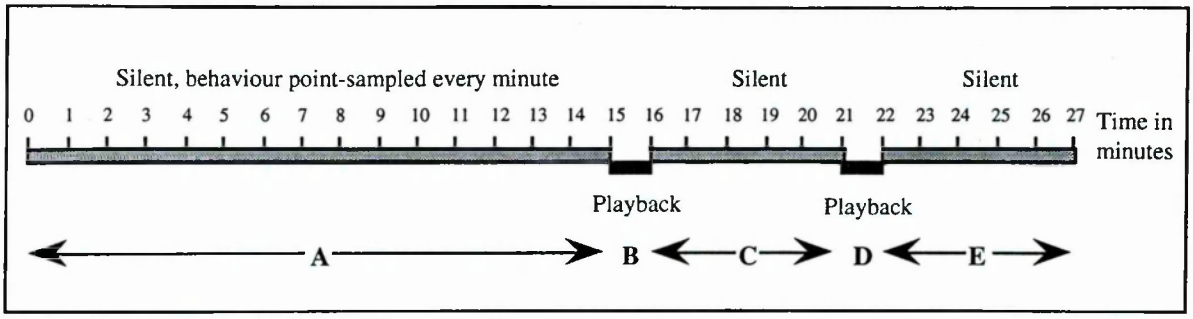


Figure 6.2. Protocol of the playback experiment. Chick calls were played for one minute during periods B and D, while the behaviour of the focal female was point-sampled every five seconds; throughout periods A, C and E no calls were played and behaviour was sampled every minute.

One 60 second playback was performed during each of two test periods (B and D), in order to increase the duration of the total sampling period for each hen. From the pilot studies described above, I found that two brief playbacks were more effective than one longer one (or several short ones) in preventing the hens becoming habituated to the chick calls. Although many hens seemed unsettled immediately after the playbacks, the five minute observation period (C) appeared to allow females to return to their usual behaviour patterns before the start of the second playback (D).

Categories of female responses

The "response" of a female was assigned to one of four categories, according to her most common behaviour pattern during the two minutes of playback (data from both periods B and D were pooled). In every case this modal group represented at least 79.2% (mean 90.76% ± 0.074) of her response behaviour patterns during the sampling periods. The four categories of response are shown in Table 6.1.

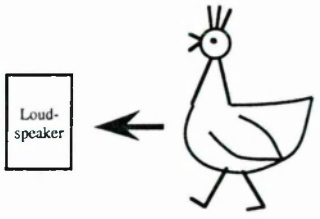
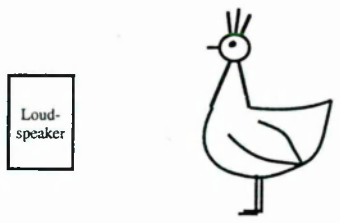
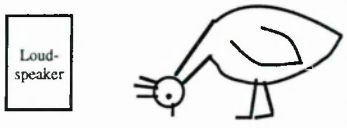
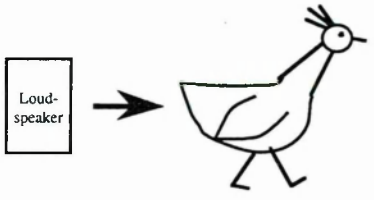
(i) "Positive" (++): female appears alert, makes brooding clucks or honks (often with neck feathers raised), and approaches the loudspeaker. 	(ii) "Interested" (+): female appears alert, but does not approach the loudspeaker. 
(iii) "Neutral" (0): no difference in behaviour observed between the silent observation periods and the playback periods. 	(iv) "Negative" (-): female shows signs of distress, and retreats from the loudspeaker. 

Table 6.1. Categories of female response to the playback of an alien chick call.

6.3.3 Results

Table 6.2 shows the reponses of females in each breeding category to an alien chick call, and the data are shown graphically in Figure 6.3. Category (a), "non breeding", includes both yearling hens and mature non-breeders, but these may be separated into (a^1), "yearling NB" and (a^2), "mature NB" (shown in Figure 6.3 in different shading). All ten "positive" responses in category (a) were displayed by yearling females. These hens however appeared inquisitive rather than broody towards the calls, approaching the loudspeaker with some alacrity and outstretched neck, but without calling (incidentally, yearling males showed a similar, if not more marked, curiosity, whereas adult males tended to ignore the playbacks) (Plate 6.5). These young individuals displayed a similar response when I played other sounds at the same volume over the speaker, such as speech or music. In contrast, the majority of mature individuals paid little attention to these latter types of playback. This suggests a general inquisitiveness on the part of immature peafowl, rather than a particular response to chick calls.

Female Category	Category of Response to Playbacks ++	 +	 0	 -	Total
(a) Non-breeding	10 (32.26)	8 (25.81)	11 (35.48)	2 (6.45)	**31**
(a^1) yearling hens	10 (76.92)	3 (23.08)	0	0	13
(a^2) mature hens	0	5 (27.78)	11 (61.11)	2 (11.11)	18
(b) Early incubation	0	5 (71.43)	2 (28.57)	0	**7**
(c) Near hatching	7 (63.64)	4 (36.36)	0	0	**11**
(d) Young brood	8 (50.00)	4 (25.00)	0	4 (25.00)	**16**
(e) Older brood	0	5 (38.46)	1 (7.69)	7 (53.85)	**13**
(f) Lost chicks	15 (83.33)	3 (16.67)	0	0	**18**

Table 6.2. Table of responses of females in each of six breeding categories to playback of alien chick calls. Category (a) has been subdivided into (a^1) yearling hens, and (a^2) mature non-breeders. Percentages of each female category displaying a particular response are shown in brackets.

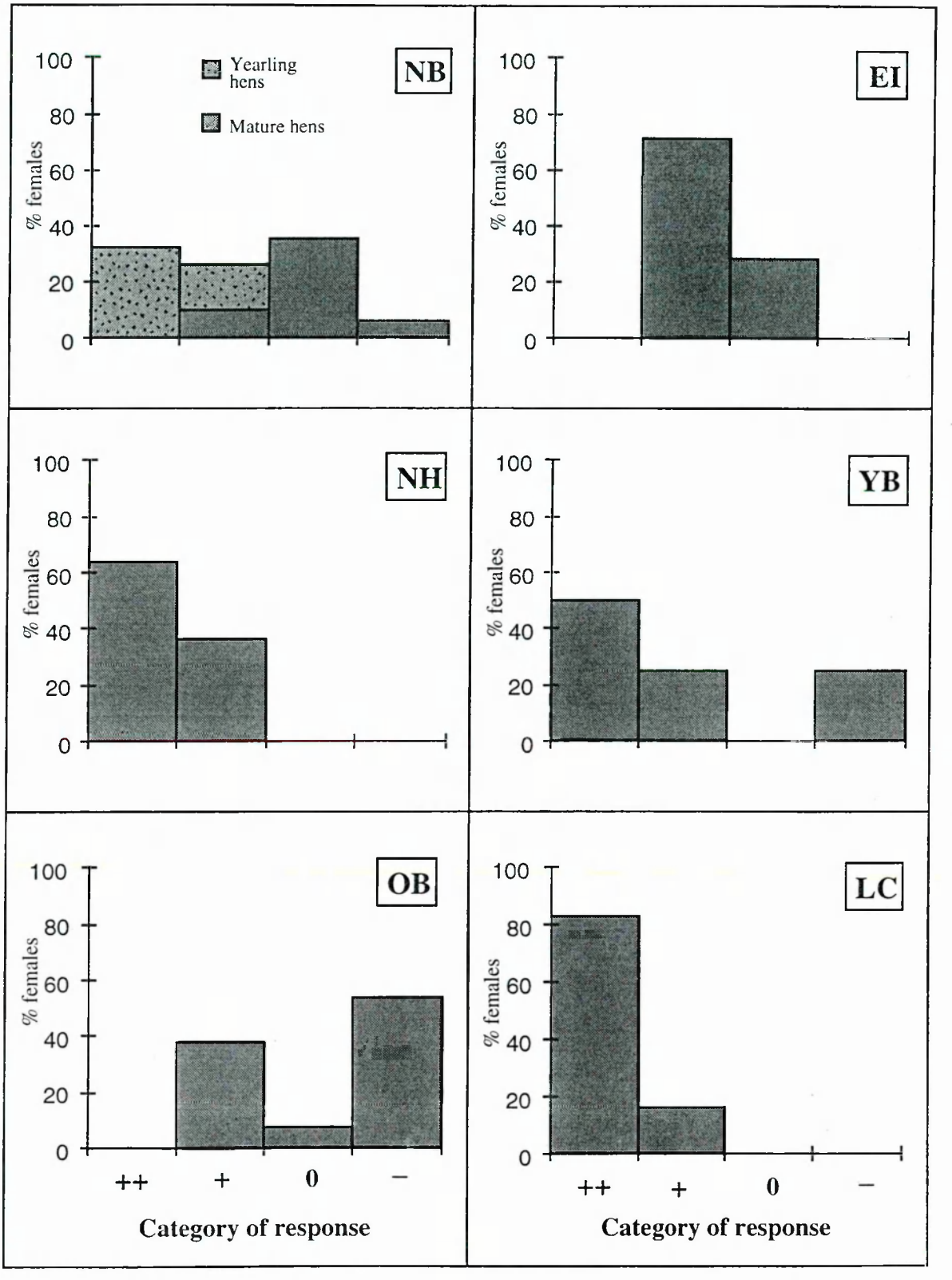


Figure 6.3. Responses of females in each of six breeding categories to playback of alien chick calls, expressed as a percentage of the total number of females in each category. As for Table 6.2, category (a) has been subdivided into yearling hens and mature non-breeders.

Plate 6.5. Immature males and females investigating a loudspeaker playing an alien chick call.

The data shown in Figure 6.3 were analysed using a "test for difference between two proportions", with corrections for continuity (test suggested by T. Lambert, Open University Statistics Department). The female category "mature non-breeders" (hereafter referred to as NB) was used as a control, and compared against each of the other five female categories, within each of the four response categories in turn. The significance level for each of the paired comparisons is given in Table 6.3.

	Category of Response to Playbacks			
Non-breeding vs:	++	+	0	-
Early incubation	0.5000	0.0588	0.1435	0.4610
Near hatching	**<0.0003**	0.4741	**0.0022**	0.3483
Young brood	**<0.0004**	0.4275	**<0.0003**	0.2451
Older brood	0.5000	0.4050	**0.0042**	**0.0145**
Lost chicks	**<0.00003**	0.3446	**<0.00016**	0.2332

Table 6.3. Significance of the differences between NB hens and each other category of female, within each response category. P-values were calculated using a test for difference between two proportions; significant differences are highlighted in bold.

The results shown in Tables 6.2 and 6.3 may be displayed more clearly as a histogram (Figure 6.4). Each response category is again considered in turn, and the proportion of females in each breeding category exhibiting that particular response can be compared. As in Table 6.3, significant differences between the control group (NB) and the other five female categories are demonstrated by asterisks.

Females that are near hatching, those with a young brood and those that have lost their chicks, are significantly more likely to display a positive response and approach the loudspeaker than the control group. There was no significant difference in the proportions of females that gave an "interested" response to the playback, although the difference between the controls and hens in early incubation was almost significant ($p = 0.0588$).

All categories of female, except those in early incubation, were significantly more likely to display some sort of response (*i.e.* not to fall into the "neutral" response category) than control females. With respect to negative responses, only hens with older broods were significantly more likely to move away from the loudspeaker than control females.

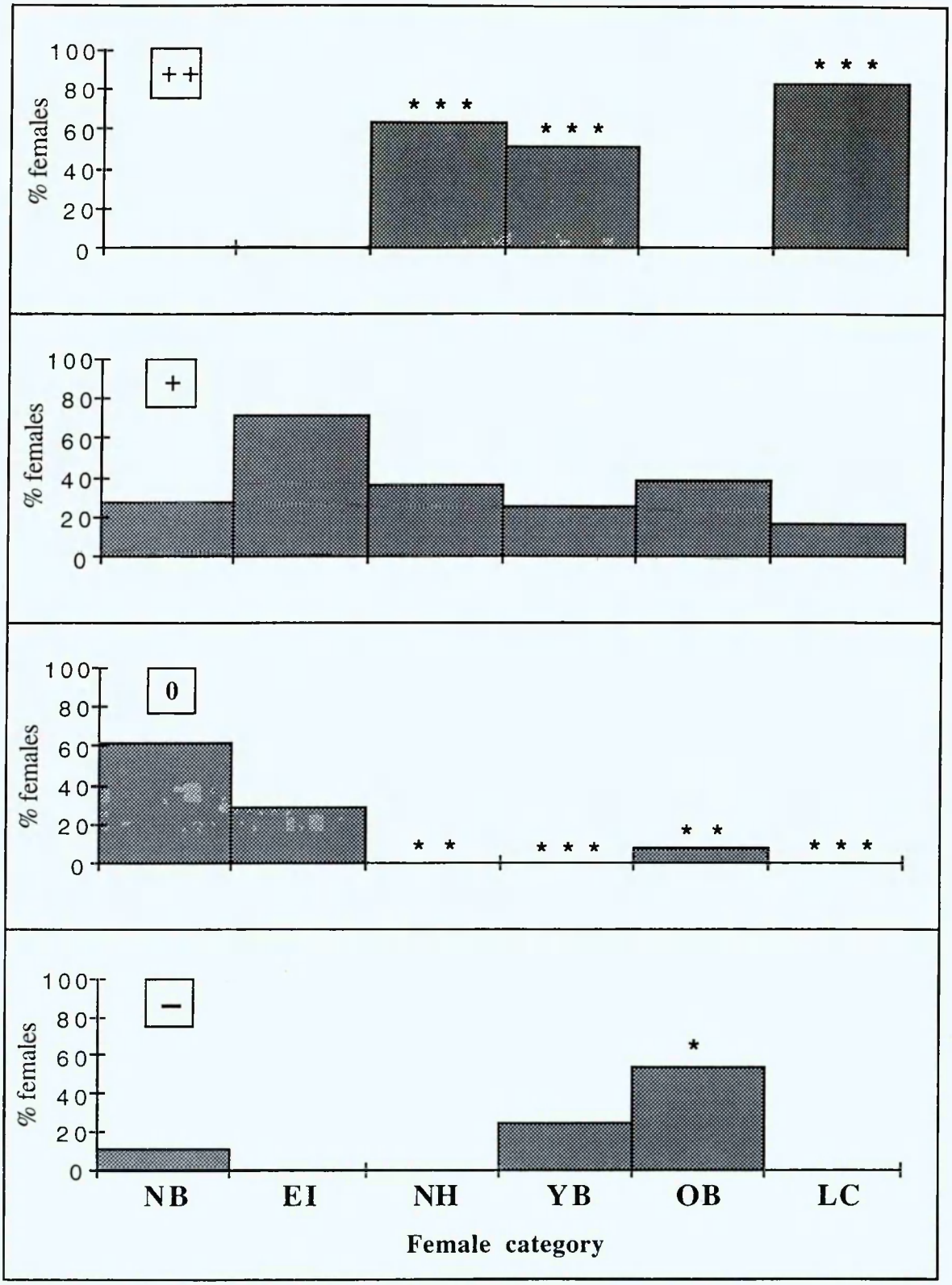


Figure 6.4. Graphic representation of the data given in Tables 6.2 and 6.3. Bar heights represent percentages of females that display a particular response, within each female category (*i.e.* as for Table 6.2). Differences between individual female categories and NB females are denoted by asterisks above the relevant columns, with the following significance levels: * = $0.05 > p > 0.01$; ** = $0.01 > p > 0.001$; and *** = $p < 0.001$ (*i.e.* as for Table 6.3).

6.4 Discussion and conclusions

Two distinct modes of alloparental care can be observed in the Whipsnade population, gang-brooding and adoption. The temporary amalgamation of broods into a gang-brood appears to have evolved as an adaptive strategy, allowing parent females to allocate more time to self-maintenance behaviour patterns and less to vigilance (Figure 5.4). In addition, the survival of their offspring is likely to be enhanced by gang-brooding; Figure 5.5 shows that in spite of a decline in individual vigilance levels, gang-broods have higher corporate vigilance (*i.e.* the probability that at least one individual is vigilant) than solitary females with broods. If, as the evidence suggests (see Section 5.3.2), vigilance does have an anti-predation function, predators are thus likely to be detected earlier by females in a gang-brood than by a solitary parent hen.

It is argued (Section 6.2.1) that the most plausible function of gang-brooding is to increase protection of the chicks against predation. There are however two apparent drawbacks to this conclusion. Firstly, hens tend to remain isolated with their brood during the first two or three days post-hatching, even though their chicks are probably most vulnerable at that age. Secondly, although the benefits of gang-brooding are predicted to increase with the number of broods involved, usually no more than two or three females are seen to amalgamate their broods. In some circumstances, gang-brood size almost certainly results from the fact that there are few females with broods in the vicinity; nevertheless, even when many parent birds are in the same paddock, similar small groups are observed. I suggest that there may be certain costs inherent in gang-brooding (*e.g.* competition, aggression, or the risk of adoption), and the observed timing and size of groups is the outcome of a cost/benefit trade-off for the individuals involved.

The other manifestation of alloparental care, adoption, is not so obviously advantageous, particularly from the perspective of the recipient female. Lazarus & Inglis (1978) suggested that in precocial species, such as the pink-footed goose *Anser brachyrhynchus* , the presence of additional young may not incur fitness costs to the adult, since all components of the parental time budget are independent of brood size (see also Williams 1994). However, it

has been demonstrated that peahens do expend more on larger broods, through feeding chicks and walking (Figures 5.6 and 5.7), and there are thus some measurable behavioural costs of adoption.

So why should peahens adopt alien young? Kin selection may play some part, but the evidence points to adoption being predominantly a consequence of "reproductive error" (Section 6.2.2). The opportunities for both deliberate and accidental adoption are many, since chicks are frequently mingled in gang-broods, but gang-brooding females are obviously not all passive recipients of stray chicks since many hens will readily attack foreign young. Such active discrimination against alien chicks obviously necessitates the development of an effective recognition system, and I suggest that the susceptibility of a female to adoption will depend upon the costs and benefits of recognising and discriminating between individual chicks.

This trade-off is in turn expected to depend upon the stage reached in the hen's breeding cycle; there are predicted to be particular "windows" within this cycle, during which it might be adaptive for a female to respond to an alien chick. Such variation can be illustrated using trade-off models similar to those presented in Figure 5.1. If the horizontal axis represents a hen's "willingness to adopt", manipulation of the cost and benefit functions can produce variation in the optimum threshold at which a hen should be inclined to accept an alien young (Figure 6.5). An increase in the benefit of adoption should result in a female adopting more readily, whereas higher cost is predicted to raise the adoption threshold.

Experimental playbacks of alien chick calls provided a useful method of testing the susceptibility of peahens to adoption; Figures 6.3 and 6.4 show that there are significant differences between the responses of hens in the various breeding categories, which supports the above hypothesis.

I suggest that these differences may correspond to variations both in the females' ability to recognise alien chick calls, and in their motivation to discriminate between chick calls when recognised. However, these factors are extremely difficult to separate at the behavioural

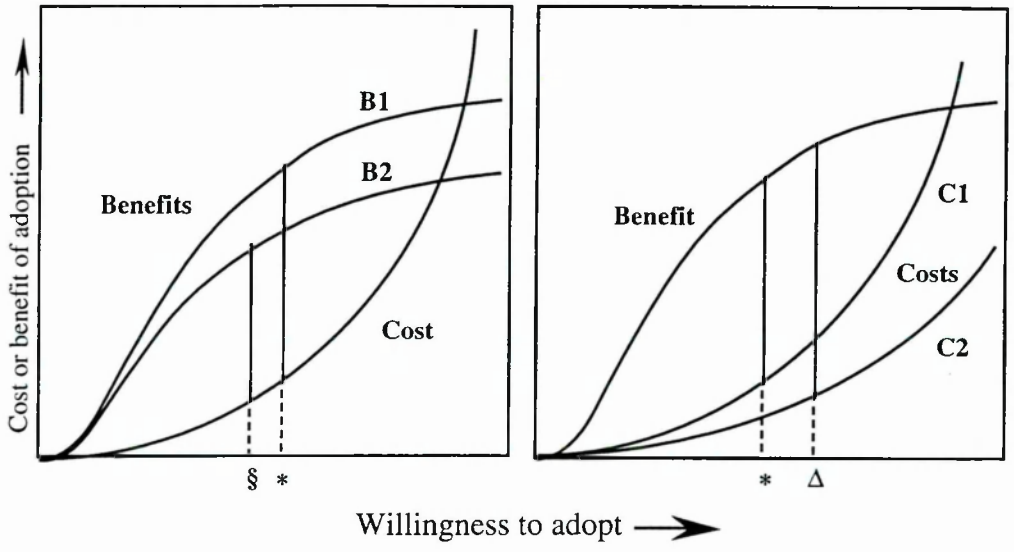


Figure 6.5. Simple cost/benefit trade-off model for adoption by peahens. As either the benefit of adoption increases (from B2 to B1), or the cost decreases (from C1 to C2), a female is predicted to be increasingly ready to adopt an alien chick (*i.e.* her willingness increases from § to * and * to Δ respectively).

level (Byers & Bekoff 1986; Barnard 1989), and it should be emphasised that at Whipsnade I could examine only the peahens' discrimination between calls, and not call recognition. Nevertheless, it seems reasonable to use such variation in discrimination as the starting point for the examination of call recognition, and hence of differential susceptibility to adoption. Using "++" as an indication of susceptibility, females most likely to adopt are those near hatching, those with a young brood, or those which have lost chicks. Similarly, using "–" as an indication of avoidance, hens with older broods are significantly less susceptible to adoption (Figure 6.4).

"Non-breeding" hens can be separated into immature and mature females (Table 6.2; Figure 6.3). As described in Section 6.3, yearling hens merely appeared curious, tending to cluster together with immature males around the speaker (Plate 6.1). In contrast, the majority (61%) of mature non-breeding hens displayed no response to the playback; a similar "indifference" was exhibited by most non-parent females towards other hens' chicks, suggesting that NB hens may be generally indifferent not only to chick vocalisations, but also to all cues presented by live peachicks (*e.g.* visual and olfactory cues).

It is possible that a non-parent hen could benefit from adoption, for example through kin selection or increased status. However, Chapter Five demonstrated that the costs of

providing parental care are considerable, and a NB hen cannot possibly mistake the playback for her own offspring. It is unlikely that the playback could represent a threat to the female, and both positive and negative responses necessitate the expenditure of time and energy. The "indifference" displayed by mature non-breeding hens thus appears to be adaptive, since the costs of responding appear to be far greater than the benefits.

"Early incubation" hens showed neither extreme positive nor extreme negative behaviour patterns; all remained sitting on the nest during the playback, but 71% of them appeared "interested", alert with head held high. In contrast, "near hatching" females, in the last three days of incubation, were far more positive in their response than EI hens. While a proportion of them (36%) remained sitting on the nest, appearing alert throughout the playback, the majority (64%) seemed rather unsettled by the calls. They stood at the nest, clucking with neck feathers erect; four hens moved towards the speaker, then returned to the nest in apparent confusion, and one female repeatedly moved between her nest and the direction of the playback.

A female with a new clutch should be strongly motivated to incubate that clutch, since at that stage incubation is the route through which she can most increase her inclusive fitness. The tendency to approach the calls of an alien chick should not therefore be selected for, since that would necessitate the hen leaving her own offspring. However, as the eggs are about to hatch, the benefits of responding to chick calls will increase (from B2 to B1 in Figure 6.5): if a peahen does not approach the call of an alien chick, she risks "ignoring" the calls of her own newly-hatched offspring, upon whose calls she has not yet imprinted. Hrdy (1977) describes a similar phenomenon in hanuman langurs *Presbytis entellus*: alloparents included females in late pregnancy, and recently parturient females, and Hrdy suggests these cases may in part be explained in tems of "priming" and endocrine changes occurring during pregnancy, which would raise the level of responsiveness to infants in general. Thus peahens in the category NH, unlike the EI females, would be hormonally "geared" for parenthood and hence more receptive to alien chick calls. An example of a hen in this category adopting an unrelated chick is given in Section 6.2.2, case history (a).

"Young brood" hens were also significantly more likely to display a positive response than NB hens, although 25% took their brood away from the speaker. Once again, these hens bear some resemblance to the "recently parturient" langur females described by Hrdy (1977), which were generally primed for motherhood and hence willing to care for alien infants. Since many YB females do not appear to discriminate between chicks, they are probably susceptible to adoption, particularly if their broods are mixing with others. An example of this situation is given in Section 6.2.2, case history (c).

Hens may be able to prevent such mixing by secluding themselves while their chicks are very young, allowing time for imprinting to occur (*i.e.* for a peahen to develop a template against which to match individual chick vocal cues and *vice versa).* Among mammals, the period following birth is often critical for female recognition of, and hence preferential attachment to, her offspring (see Section 6.1.3), and mistaken identity is most likely to occur in synchronous and dense breeders, such as a number of seal species (*e.g.* Riedman & Le Boeuf 1982; Boness 1990). The females of some species demonstrate "preparturition seclusion", which may have the function of allowing the development of a recognition system before the young start to mix with others (*e.g.* Laws & Clough 1966; Rudge 1970; Dagg & Foster 1976; but see *e.g.* Gosling 1969).

The development of imprinting may help to explain why chicks are not usually gang-brooded for the first two or three days post-hatch, even though this period is probably when they are most vulnerable to predation. Parental discrimination between young has been reported to occur within the first two weeks post-hatch in geese (Ramsey 1951; Prevett & MacInnes 1980), and, like peafowl, adoptions are common in these precocial species. However, unlike peafowl, adoption persists for at least several weeks after parent-offspring recognition has developed in the lesser snow goose *Chen caerulescens caerulescens* (Williams 1994), the Canada goose *Branta canadensis* and the barnacle goose *Branta leucopsis* (Choudhury *et al.* 1994). It appears that the costs of adoption in geese may be lower than potential costs recorded in peafowl (adoption even appears to be beneficial in some goose populations), and consequently that there is little selective pressure for rejection of alien goslings (Lazarus & Inglis 1978; Williams 1994).

"Older brood" females were the only category to display a significantly negative response to the playback. Since no OB females approached the loudspeaker, it can be deduced that these hens may be less susceptible to adoption than those in the categories NH, YB or LC. Similar results have been found in guanacos and llamas, in which mothers with older young rarely foster aliens (Pilter 1954), but the same is not true for several species of geese (see above).

"Lost chicks" hens showed the strongest positive reaction to the playbacks of all of the categories observed. Five of the 18 females in this category had lost their broods through natural causes; three of these appeared merely "interested", while the other two moved towards the speaker. All of the 13 hens whose chicks I had temporarily taken for marking were in the "++" category, many of them actually running towards the playback, honking loudly. Some females had been callling intermittently following the removal of their broods, but as soon as the playback started their rate of calling increased as they approached the speaker. In fact, females whose chicks I had collected were so ready to respond to *any* chick calls, that I was able to use this fact to return marked chicks safely to their mother - I could merely whistle an approximation to a chick's distress call, and the female would often come running to my "cheep imitation"!

In common with hens in categories NH and YB, the behaviour patterns displayed by LC females support the hypothesis that adoption is the result of errors of recognition, leading to "misplaced parental behaviour" (Williams 1966a). Such errors could occur, for instance, if the hens are physiologically and behaviourally prepared to provide parental care towards any young (Hrdy 1977; Riedman 1982); the costs to hens in these categories of not approaching a lone, distressed chick, which may be their own offspring, may outweigh the potential costs of adopting an alien young.

The tendency for LC hens to care for young appears to decline over time, as illustrated by the fact that females which had lost chicks within the previous hour (*i.e.* I had removed them) were more likely to respond very positively to playbacks than those which had been without chicks for more than a day. However, one example of adoption by such a female is given in Section 6.2.2, case history (b), in which a hen (B39) which had lost her brood

when they were two or three days old was almost immediately seen closely associating with another female (B45) and her young brood. More than a week later, B39 permanently adopted one of B45's chicks; demonstrating that the motivation to care for young can persist for some considerable time after the loss of a brood.

The evidence presented here supports the idea that there is some cost of adoption to peahens, and that an effective parent-offspring recognition system develops some time between a few days and three weeks post-hatch. The development of vocal identification cues before the onset of gang-brooding would assist the hen in maintaining cohesion with her own brood, and avoiding responding to alien chicks. In the gang-broods, the behaviour of the chicks towards the peahens could also aid the peahens in the recognition of their offspring; however, for the purposes of the experiment described in Section 6.3 the "chick behaviour" factor was removed, and hens were responding solely to vocal cues (Holley 1984; Knudsen & Evans 1986).

Although this investigation has revealed something of the nature of chick recognition and adoption in peahens, a fuller understanding could be achieved from some additional experimental work (although perhaps in a more confined and accessible study area than Whipsnade). Playbacks of calls provide a useful measure of kin discrimination on the basis of vocal cues, since the behaviour of the caller is not a confounding factor. Further experiments might include playbacks of "own *vs* alien" chick calls, matching the ages of the calls used in the choice test. In addition, nothing is known of the recognition of peahens by their offspring; female calls, for example, are much more complex than chick cheeps, and therefore probably provide a more reliable "signature" as a recognition cue (if young chicks have the capacity to process that information). Similar choice tests could therefore be presented to chicks, at various ages, to examine whether they can discriminate between "own *vs* alien" parents.

Conclusions

Gang-brooding behaviour in the Whipsnade population appears to be an adaptive strategy against chick predation, allowing peahens to reduce their individual vigilance levels while

increasing the corporate vigilance of the group. Two factors seem to contradict this conclusion, however: gang-broods are generally smaller than the optimum predicted size, and gang-brooding does not usually occur during the initial two or three days post-hatch, when the chicks are most vulnerable.

It is suggested that observed gang-brood sizes may be the outcome of a trade-off between the benefits of increased safety, and the costs of amalgamation, including adoption. Playback experiments show that females with clutches close to hatching, or with very young broods, are particularly responsive to the calls of an alien chick, indicating that they may be more susceptible to adoption. It may thus be adaptive for peahens to remain solitary around the time of hatching, allowing the opportunity for an adequate parent-offspring recognition system to develop.

Adoption does not appear to be an adaptive strategy in peahens; rather, it seems that there are particular "windows" in the hen's breeding cycle when she is more responsive to alien young, and these windows occur when the costs of rejecting or attacking an alien chick outweigh the costs of accepting it into her brood. The costs of rejection will be higher when there is increased likelihood that the chick is one of the female's own, such as when imprinting is not fully developed, or when a female has lost her own chick(s). Observations support this conclusion; females most likely to respond are those with offspring around hatching, and those who have lost chicks.

In summary, the two forms of alloparental care displayed by hens at Whipsnade are rather different: gang-brooding appears to be an adaptive anti-predation strategy, whereas adoption is the response to constraints of recognition.

CHAPTER SEVEN
SUMMARY AND CONCLUSIONS

7.1 Introduction

This thesis describes a detailed investigation into the parental behaviour of the Indian peafowl, using a large feral population at Whipsnade Wild Animal Park, Bedfordshire. The peahen makes an useful subject for the study of parental investment, since hypotheses regarding relative levels of expenditure are simplified by the fact that the female is entirely responsible for care of the precocial chicks.

Parental investment was examined from the onset of incubation (Chapter Three) until after the chicks had fledged (Chapters Four and Five), and both material measures (*e.g.* the allocation of resources to eggs) and behavioural measures (*e.g.* brood defence and time spent on parental behaviour patterns) were used. Expenditure was studied in relation to a range of variables, including the reproductive value of parent and offspring, and various physiological, ecological and life history constraints.

Current theory predicts that parents should invest according to their own residual reproductive value, as well as to the value of their offspring (Williams 1966b; Pianka 1976; Curio 1983; Winkler 1987). Individuals of long-lived species displaying age-related mortality are expected to increase their level of parental expenditure as they grow older, and their residual reproductive value declines (see Section 1.3.3). This prediction can be confounded by various factors such as parental experience, or constrained by physiological condition (*i.e.* even if an individual increases its effort over subsequent seasons, the resources available for reproduction may decline), and observed levels of expenditure may therefore increase, decrease or show no variation with parental age.

Hypotheses regarding investment in relation to offspring reproductive value can suffer from similarly confounding variables. For example, offspring are predicted to become more valuable as they grow older and increase their probability of survival to breeding age, and

parental expenditure should therefore increase with chick age; however, the benefits of parental care to offspring fitness will generally decrease with chick age, which favours a decline in expenditure. In addition, expenditure might be expected to decrease over a breeding season, since offspring born early in the year are of higher value than late-hatched chicks; yet the opposite trend is predicted if parents increase their investment in relation to declining renesting potential over the season. The effects of clutch or brood size on parental investment can also depend on a range of factors, such as trade-offs with egg or chick size, the type of investment involved (shared or unshared), and in the case of unshared offspring defence, both the type of predation usually experienced (brood loss or fixed loss) and the risk taken by the parent (Lazarus & Inglis 1986).

In this investigation of parental expenditure in the peahen, I have aimed to remove or account for as many potentially confounding variables as possible, and to measure investment expressed as a variety of behaviour patterns. Observations were also made on other manifestations of parental care, particularly pre- and post-hatch brood amalgamation (Section 3.4 and Chapter Six respectively), and these are discussed with respect to possible costs and benefits of alternative strategies.

7.2 General discussion

The relationships between levels of parental expenditure, and a range of variables relating either to reproductive value or constraints, are summarised in Table 7.1. The data presented in Chapters Three, Four and Five were tested using both non-parametric and multivariate analysis; since in almost every case both analyses indicated that the same variables were the most important predictors of variation in parental expenditure, Table 7.1 shows the simpler, non-parametric relationships (exceptions will be discussed individually below). Investment in nesting is examined using two material measures of expenditure, egg size and clutch size, as well as several behavioural measures: date of lay, vigilance during incubation, absence from the nest, and time spent turning eggs. The expenditure of hens with broods is examined using behavioural measures of brood defence, vigilance, feeding chicks and walking with the brood. Factors indicating parental and offspring reproductive value,

vulnerability and constraints, are listed vertically in Table 7.1, and their effect on each of the measures of expenditure are also shown. Both the predicted and the observed direction of each individual relationship is given, together with the significance levels of the observed relationships.

Variable	P.I.	Egg size	Clutch size	Date of lay	Vigil. (incub)	Nest attend.	Turn eggs	Brood defence	Vigil. (brood)	Feed chicks	Walk (brood)
Female age	P	+	+	–	+	+	+	+	+	+	+
	O	–	–	+	–	–	–	+	+	–	–
	Sig.	○	○	★★	○○	○	○	○	○	○	○
Female weight	P	+	+	–	+	+	+	+	+	+	+
	O	+	+	–	+	+	+	+	+	–	+
	Sig.	○	○	○	★★	○	○	★	○	○	○
Time season (RV) ①	P	–	–		–	–	–	–	–	–	–
	O	–	–		–	+	–	–	+	+	–
	Sig.	★★★	★★★		★	○	○	○	★★	○○	○
Time season (RP) ②	P	+	+		+	+	+	+	+	+	+
	O	–	–		–	+	–	–	+	+	–
	Sig.	★★★	★★★		★	○	○	○	★★	○○	○
Egg volume	P		–		+	+	+				
	O		+		+	+	+				
	Sig.		★		★	○○	○				
Clutch size ③	P				+	+	+				
	O				+	+	–				
	Sig.				★★★	○	○				
Incub. stage ④	P				+	+	+				
	O				+	+	–				
	Sig.				○	★	★				
Chick age (RV) ⑤	P							+	+	+	+
	O							–	–	–	+
	Sig.							★★★	★★★	★★★	★
Chick age (V) ⑥	P							–	–	–	+
	O							–	–	–	+
	Sig.							★★★	★★★	★★★	★
Brood size (Sh) ⑦	P							+	+	+	+
	O							+	+	+	+
	Sig.							★★★	○	★★	★★
Brood size (Un) ⑧	P							o	o	o	o
	O							+	+	+	+
	Sig.							★★★	○	★★	★★

Table 7.1. Summary of results reported in this thesis. Column headings refer to the measures used to examine levels of parental investment (P.I.); row headings refer to a range of ecological, physiological and life history variables measured. The directions of both predicted (P) and observed (O) relationships are shown. "+" represents a positive relationship, "–" a negative relationship, and "o" no relationship. The significance (Sig.) of each observed relationship is described as follows: ○ indicates $p>0.1$; ○○ indicates $0.05<p<0.1$; ★ indicates $0.01<p<0.05$; ★★ indicates $0.01<p<0.001$; ★★★ indicates $p<0.001$. Notes: ① Reproductive value (RV) theory predicts a decline in P.I. over the season; alternatively, ② as renesting potential (RP) declines, investment is predicted to increase. ③ Since nest predators at Whipsnade either destroy whole clutches, or cause the female to desert, it is argued that both shared and unshared investment should increase with clutch size. ④ Incubation stage is equivalent to egg age, and therefore offspring reproductive value. ⑤ Reproductive value (RV) theory predicts an increase in P.I. with chick age, whereas ⑥ if hens invest according to offspring vulnerability (V), expenditure should decline with chick age in precocial species. ⑦ Shared investment (Sh) is predicted to increase with brood size, whereas ⑧ unshared expenditure (Un) should be independent of brood size, since predators at Whipsnade generally take single chicks. For details, refer to relevant chapters.

Female age and weight

It can be seen from Table 7.1 that peahens do not appear to be investing in accordance with their own residual reproductive value; all except two of the relationships are in the direction opposite to that predicted, and only one of these unexpected results is significant (young hens lay significantly earlier in the season than older hens). The assumptions upon which the theory is based might not be applicable to peahens at Whipsnade, since hens do not continue to grow once they have reached breeding age, and survival has not been demonstrated to decline with parental age. It is therefore possible that once a female reaches maturity, her expectation of mortality (and consequently her expenditure) may remain constant until approaching the end of her expected lifespan.

Table 7.1 shows that female weight is not significantly related to the majority of behavioural and material variables measured; only two relationships are significant, indicating that heavy hens are more vigilant throughout incubation, and more defensive against predators, than lighter hens. These results support the conclusion that expenditure is constrained by female weight, and even within the non-significant variables there is an apparent trend for heavier hens to invest more. It was suggested in Section 5.4 that female weight may be more of a constraining factor in behaviour patterns that are more expensive, in terms either of energetic cost, or of parental mortality risk. Investment in brood defence may depend upon the probability that a hen can successfully defend her brood against a predator, while ensuring her own survival, and this probability may well be related to female body size. A mixture of strategies may thus be the outcome; it could be adaptive for heavy females to stay and defend their broods, whereas lighter hens would benefit more from fleeing and thereby surviving to breed again. Such a variety of responses should be selected for only if the predator was a threat to the adult peahen as well as to her brood, but it is not unlikely that an approaching human (myself) could be regarded as such a threat.

It is more difficult to justify the argument that vigilance on the nest is either energetically expensive or hazardous, but it is possible that hens in better condition have larger or higher quality clutches, which warrant greater investment. Indeed, multiple regression analysis (Table 3.3) shows that clutch size is the only important predictor of vigilance during

incubation, and all other factors operate through this variable. Female weight therefore appears to be important in only one measure of parental expenditure, brood defence. However, it is difficult to draw any firm conclusions about age- or condition-related investment from these results, since the data were extracted from previous capture records and are therefore necessarily crude estimates of relative differences; nevertheless, there is some indication that the influence of female weight on parental expenditure is more important than the effect of female age.

Time in breeding season

Parental expenditure on egg size, clutch size and vigilance during incubation, declines significantly over the breeding season, thereby lending support to the hypothesis that peahens are investing in accordance with their offsprings' reproductive value (RV). This hypothesis assumes that chicks hatched early in the year have a greater chance of survival, and a longer potential growth period before first breeding, than late-hatched chicks, and are therefore of higher value. However, the allocation of resources to the size and number of eggs is not necessarily an adaptive strategy; it is also likely to be related to a range of proximate environmental factors, such as food availability or nest cover. Several alternative explanations for a decline in material expenditure over the season are discussed in detail in Section 3.6; it is concluded that the three most convincing hypotheses appear to be that replacement clutches are smaller than initial nesting attempts, that lighter hens nest later than heavy hens and lay smaller clutches, and that nest parasitism by older females constrains or allows them to lay fewer eggs in their own nests later on (the last of these possibilities will be examined further below).

With respect to vigilance at the nest, the function of such a behaviour pattern will affect variation in its expression. If hens are looking out for nest predators, according to reproductive value theory early clutches are worth more than later ones, and hens should be more vigilant early on (assuming no changes in predation rates). The same trend is expected, however, if they are on guard for nest parasites, since intraspecific nest parasitism has been shown to be more prevalent at the start of the season (Section 3.4.2). Evidence

presented below suggests that the function of vigilance during incubation is more likely to be anti-predation than anti-parasitism.

The above observations are apparently contradicted by the increase in the time spent on vigilance by hens with chicks as the season progresses, which supports the "renesting potential" (RP) hypothesis; *i.e.* as the opportunities available for renesting diminish, the current brood becomes increasingly more valuable. It was concluded in Chapter Five that the function of vigilant behaviour by parental hens is predominantly to prevent predation of the chicks. It would therefore be desirable to take account of variation in predation pressure over the season, in order to discover whether peahens genuinely invest more in later broods.

It is evident that attempting to test predictions of how parental expenditure varies over a breeding season can lead to a minefield of conflicting and confusing data. The results presented in Table 7.1 do not provide conclusive evidence for either the reproductive value or the renesting potential hypothesis, since some measures of expenditure increase and others decrease over the breeding season. For example, it is possible that neither hypothesis is correct; or that both factors are influencing parental effort over the season but in opposite directions. Further investigation is necessary in order to discriminate between these two hypotheses, but it is difficult to see how this could be achieved, through either experimentation or observation. Experimental studies such as brood manipulation would be rather impractical in the field, but one starting point would be to determine which additional factors (*e.g.* predation pressure, food availability or vegetative nest cover) might affect each of the measures of expenditure, and to ascertain how these may vary throughout the year.

Clutch parameters

There is no apparent trade-off between the size and number of eggs within the Whipsnade population, since both are correlated positively (though non-significantly) with female weight and negatively with the date of lay. At an individual level, females are far more consistent with respect to egg volume than clutch size, suggesting that for each individual hen, either egg size is constrained (*e.g.* by oviduct dimensions), or there is a narrow range of optimal sizes. The hypothesis that females increase propagule size to produce larger,

fitter offspring as environmental conditions deteriorate is refuted by the observed decline in egg size over the season.

The time allocated by peahens to vigilant behaviour is positively correlated with egg volume, clutch size and incubation stage, but multiple regression analysis reveals that clutch size is the only significant predictor of vigilance levels in peahens. This observation supports the prediction of Lazarus' & Inglis' (1986) hypothesis: although vigilance against predators is considered to be an unshared component of parental invesment, its relation with the number of offspring will depend upon the typical form of predation (see "Brood size", below). Since nest predators at Whipsnade generally destroy the entire clutch when they strike, and even partial predation causes the female to desert, the benefit to the hen of detection increases with the number of offspring and vigilance is predicted to increase with clutch size.

In contrast, if the function of vigilance is to prevent nest parasitism, there is no predicted relationship with clutch size, since the behaviour pattern is "unshared" and only one egg is deposited at a time (*cf.* the "fixed loss" case of brood predation: Lazarus & Inglis 1986). However, larger clutches are significantly more likely to be parasitised than small clutches (Figure 3.28); if parasitism occurs during the incubation period, vigilance might be expected to increase with clutch size; but if larger clutches are more susceptible simply because of their longer unguarded laying period (see Section 3.4.2), vigilance levels during incubation should be irrespective of clutch size. Even if parasitism does occur after the onset of incubation, it seems improbable that hens with larger clutches should be more vigilant for parasites, since deposition does not occur in the presence of the sitting hen. In conclusion, the positive relationship between vigilance and clutch size suggests that detection of predators is the most likely function of vigilance during incubation.

Attendance at the nest increases (though not significantly) with clutch size, egg volume and stage of incubation. Multiple regression analysis reveals, however, that levels of attendance cannot be significantly predicted by the variables measured, although the most important variables are egg volume and incubation stage (Table 3.3). These data tend to support the hypothesis that hens are investing in accordance with the reproductive value of the clutch, although there are alternative explanations: for example, the costs of reheating larger eggs or

clutches may be greater, and time spent absent from the nest may be decreased in order to minimise this effect; embryos in the later stages of development may suffer more from cooling, or may be more vulnerable to predation as they start to pip in the shell; or hens may be more attentive as incubation progresses, in order to reduce the probability of being absent when the chicks hatch.

The multiple regression model for predicting the time allocated to turning eggs is even less significant than that for nest attendance, but the most important predictor variables are clutch size, incubation stage and female weight (Table 3.3). All of these variables are negatively related to egg turning, and thus tend to contradict the hypothesis that females invest more in clutches of higher reproductive value.

In conclusion, of the three behavioural measures of expenditure on clutches, only vigilance provides significant evidence for the hypothesis that peahens invest according to the reproductive value of their clutch. Observed levels of nest attendance are also correlated with clutch variables in the predicted direction, although the relationships are not significant; in contrast, time allocated to turning eggs declines as expected clutch reproductive value increases (again, not significantly), and since no adaptive explanation can be given for this rather surprising result, it is suggested that certain physiological or ecological constraints may be more important in determining egg rolling behaviour patterns.

Chick age

The reproductive value hypothesis predicts that parents should invest more in older offspring, since they have a greater chance of surviving to reproduce. The vulnerability hypothesis predicts the opposite: as offspring grow older, they become more independent and better able to care for themselves, and the benefits of parental care decline; thus parental expenditure is expected to decrease with chick age. There is strong evidence from the behavioural measures summarised in Table 7.1 that peahens at Whipsnade are adjusting their expenditure in relation to chick vulnerability, rather than to chick reproductive value.

Parental investment in brood defence was investigated in Chapter Four, and it was shown that almost all of the variation in observed levels of defence is explained by chick age,

although brood size and female weight are also influential (Table 4.3). Table 5.7 likewise demonstrated that vigilance levels are related primarily to chick age and group size, but that time in season also has some effect. Since it was concluded in Chapter Five that the principal function of vigilance by peahens with broods is to scan for predators of the chicks, it is perhaps not surprising that these two measures of parental effort, vigilance and defence, are similarly correlated with chick age.

The two other measures of parental expenditure by peahens with broods, feeding chicks and walking, are significantly related to only two variables: chick age and brood size. The proportion of time allocated to feeding chicks declines with chick age, which supports the hypothesis that females are investing in relation to the chicks' increasing self-sufficiency. Time spent walking with a brood increases with offspring age, but this observation is in agreement with both the reproductive value and the self-sufficiency hypothesis, since the expression of this behaviour pattern is controlled not only by the parent but also by the chicks' ability to walk. Nevertheless, expenditure by females on the care of chicks appears to be adjusted to the benefits of such care to the offspring, rather than its benefits to the parent; *i.e.* younger, more vulnerable chicks benefit more than older chicks from parental defence, vigilance, and feeding.

Brood size

The hypotheses tested concerning the effect of brood size on parental expenditure are based upon the predictions given by Lazarus & Inglis (1978, 1986), for shared and unshared forms of investment. Optimal levels of shared investment, for both parent and offspring, are predicted to increase with brood size. The majority of unshared forms of investment consist of anti-predator care, and the relationship with brood size will depend upon the type of predator usually encountered. If a predator typically takes the entire brood, the benefit to both parent and offspring of investment in defence will increase with brood size; if a predator generally takes a single offspring at a strike, the optimum level of expenditure for the parent will be independent of brood size, whereas the optimum for the offspring will decrease through simple prey dilution. Parent-offspring conflict over shared investment is predicted to increase with brood size, but to decline for unshared investment. However,

many of the anti-predator forms of parental care (*e.g.* vigilance) are assumed to be under the control of the parent, and therefore to change with respect to brood size in accordance with parental optima.

It was concluded in Chapters Four and Five that the behaviour patterns of brood defence and vigilance are both unshared, anti-predator forms of parental investment, and that time spent feeding chicks will be shared if chicks are fed individually, but unshared if food is merely pointed out to the whole brood. It is more difficult to categorise the behaviour pattern of walking with the brood, since that will depend upon its function; it was argued in Section 5.4 that the most likely function of walking is to seek out new food patches for the chicks.

Predators of precocial species such as peahens typically take single chicks, and levels of anti-predator care are thus expected to be independent of brood size. However, multiple regression analysis reveals that brood size has a significant effect on the levels of brood defence displayed, in contrast with predictions for unshared parental investment. It was suggested in Section 4.4 that larger broods may be defended more because of their greater cumulative value; because they take longer for the hen to collect together; or because the hens regard me (the "predator") as a threat to the entire brood rather than to individual chicks. This observation highlights the danger of making general conclusions about parental expenditure on defence from experimental studies, if the type of predator used to test defence is not one that the subject would encounter naturally.

The proportion of time allocated to vigilance is not significantly related to brood size (Tables 5.4 and 5.7), thus supporting the predictions of Lazarus' & Inglis' model for unshared expenditure. Chick feeding behaviour is positively correlated with brood size, and therefore also appears to support the model for shared investment; however, brood size is confounded by chick age, and the relationship with feeding is significant only for the youngest chick category. It is suggested that newly hatched chicks need to be fed individually, so that chick feeding behaviour is shared, but the chicks' increasing ability to feed themselves shifts the nature of parental investment along the scale from shared towards unshared.

The observation that time spent walking with a brood increases with brood size indicates that the behaviour pattern is shared, and that hens may be searching for food for their brood. The relationship is however confounded by chick age, and is non-significant in the youngest age category. It is suggested that, since a newly hatched brood is probably unable to walk far, the time spent walking by its parent will be low and independent of brood size. As the chicks grow, not only can they walk further, but they also require more food, and parental expenditure on time spent walking thus shifts along the scale from unshared towards shared as the chicks grow older.

Brood amalgamation

Peahens at Whipsnade demonstrate two main forms of brood amalgamation, pre-hatch (Section 3.4) and post-hatch (Chapter Six). Pre-HBA can be further divided into dump nesting and intraspecific nest parasitism (INP), and post-HBA is manifested as gang-brooding and adoption.

Pre-hatch brood amalgamation has been examined in detail in Section 3.4, and it appears that the two strategies may be related, particularly since both occur at the start of the breeding season. The deposition both of single eggs and of large dump nests initially appears extremely maladaptive, since these eggs are never incubated. It is suggested that both behaviour patterns may be the result of physiological or environmental constraints, and dump nests may be a misguided attempt at INP. Dumped eggs are significantly larger than incubated eggs, even after removing the influence of the decline in egg size over the season, but there is no obvious adaptive explanation for this phenomenon.

Eggs laid by nest parasites are significantly larger than non-parasitic eggs, but are not significantly larger than host eggs within parasitised clutches. Host clutches are larger, contain larger eggs, and occur earlier in the season than non-parasitised clutches, but multiple regression analysis reveals that of the variables measured, clutch size is the only important predictor of whether a clutch will be parasitised or not. It is suggested that larger clutches are more susceptible to INP because they take longer to lay, during which time the nest is unguarded.

Intra-clutch variation in eggs is lower than inter-clutch variation, but this does not appear to result in the rejection of foreign eggs. Possible adaptive explanations for the acceptance of alien eggs assume that the costs of rejection are higher than the costs of acceptance, perhaps because the risk of ejecting a host egg is greater than the cost of caring for a larger clutch (and brood). Young females nest earlier in the season than old females, and it is suggested that old hens may be parasitising the nests of young ones, before laying their own clutch. The hatching success of parasitic eggs is considerably lower than either host eggs or non-parasitised clutches, but if INP exists as part of a mixed strategy, overall chick production may be enhanced.

Gang-brooding behaviour in the Whipsnade population appears to be an adaptive strategy against chick predation, allowing peahens to reduce their individual vigilance levels while increasing the corporate vigilance of the group. Two factors seem to contradict this conclusion, however: gang-broods are generally smaller than the optimum predicted size, and gang-brooding does not usually occur during the initial two or three days post-hatch, when the chicks are most vulnerable.

It is suggested that observed gang-brood sizes may be the outcome of a trade-off between the benefits of increased safety, and the costs of amalgamation, including adoption. Playback experiments show that females with clutches close to hatching, or with very young broods, are particularly responsive to the calls of an alien chick, indicating that they may be more susceptible to adoption. It may thus be adaptive for peahens to remain solitary around the time of hatching, allowing the opportunity for an adequate parent-offspring recognition system to develop.

Adoption does not appear to be an adaptive strategy in peahens; rather, it seems that there are particular "windows" in the hen's breeding cycle when she is more responsive to alien young, and these windows occur when the costs of rejecting or attacking an alien chick outweigh the costs of accepting it into her brood. The costs of rejection will be higher when there is increased likelihood that the chick is one of the female's own, such as when imprinting is not fully developed, or when a female has lost her own chick(s). Observations

support this conclusion; females most likely to respond are those with offspring around hatching, and those who have lost chicks.

The behaviour patterns of nest parasitism and adoption have many similarities, since both appear to be maladaptive from the host female's perspective, and to depend upon her ability to recognise and her motivation to discriminate between offspring. It has nevertheless been demonstrated that peahens in this situation are probably behaving optimally, accepting alien eggs or chicks because the costs of acceptance are lower than the costs of rejection or desertion. The possible causes and functions of these complex phenomena are necessarily the subject of conjecture, but the identification of parasitic and host females, eggs and chicks, for example by observations or genetic fingerprinting, would be extremely useful in the examination of brood amalgamation at Whipsnade.

7.3 Conclusions

- **Is parental expenditure related to the residual reproductive value of the parent, or to the detrimental effects of that expenditure on parental fitness?**

Parental expenditure is not correlated with female age; female weight also has little influence on parental investment, except with respect to the more demanding forms of expenditure such as brood defence, when it may act as a constraint. The hypothesis that hens increase investment with declining residual reproductive value is therefore not supported, and it is suggested that the assumptions upon which this theory is based may not be applicable to the peahens at Whipsnade, since there is no evidence of increasing mortality risk with parental age over the majority of the hen's lifespan. There is however some limited indication that expenditure may be related to the costs of investment to parental fitness.

- **Is parental expenditure related to the reproductive value of the offspring, or to the beneficial effects of that expenditure on offspring fitness?**

Nest attendance increases with measures of clutch reproductive value, but the overall relationship is not significant. In contrast, egg rolling declines slightly with these measures,

suggesting that physiological or ecological constraints may be more important determinants of egg rolling than clutch reproductive value. All four behavioural measures of parental expenditure in broods (brood defence, vigilance, feeding chicks and walking) decline with chick age, suggesting that investment is adjusted to chick vulnerability rather than to chick reproductive value.

Material investment in egg volume and clutch size declines over the breeding season, but although this supports the hypothesis that females are investing in relation to the reproductive value of their brood, other explanations (particularly differential laying dates) are also likely. Other behavioural measures of investment do not vary predictably over the season, suggesting that hens do not invest in accordance with either offspring reproductive value or renesting potential individually; alternatively, both factors may be influential, but in opposite directions. Further experiments are necessary in order to discriminate between these contrasting hypotheses.

The evidence therefore indicates that for many forms of parental care, the level of expenditure displayed by a peahen may be determined predominantly by the benefits of that care for the offspring, as opposed to the benefits for the parent.

- **Does parental expenditure vary with clutch/brood size in accordance with the predictions for shared and unshared parental investment?**

Vigilance levels increase with clutch size, which supports the hypothesis that vigilance is an unshared form of anti-predator behaviour, in which predators typically take the entire clutch simultaneously. Brood defence is positively correlated with brood size, thus countering the predictions for unshared, fixed-loss forms of investment; it is suggested that larger broods may take longer to collect, or hens may regard me (the "predator") as a risk to the entire brood.

Parental vigilance declines with increasing group size and chick age, but is unrelated to brood size; this supports the predictions for unshared, fixed-loss forms of investment, and suggests that the function of vigilance is to prevent predation of the chicks. Chick feeding behaviour increases with brood size, but is significant only for very young chicks; it is

suggested that as chicks develop the ability to feed themselves, chick feeding moves along the continuum from shared towards unshared investment. Time spent walking increases with brood size, and the suggested function is to search for food; the relationship is not significant for newly hatched chicks, and it is suggested that as chicks improve their walking ability and require more food, walking shifts along the scale from unshared towards shared expenditure.

These observations suggest that Lazarus' & Inglis' (1986) parental investment theory can correctly predict the relationship between clutch or brood size and most forms of parental expenditure. The results also demonstrate that parental care need not be defined permanently as either shared or unshared, but can move along a continuum between the two categories.

- **Is brood amalgamation an adaptive strategy?**

Peahens exhibit both pre-hatch brood amalgamation (dump nesting and nest parasitism) and post-hatch brood amalgamation (gang-brooding and adoption). Dump nesting may be a response to physiological or environmental constraints, or it may be a misguided attempt at nest parasitism. Large clutches are selectively parasitised, probably because of their longer unattended laying period. The hatching success of parasitic eggs is lower than host or non-parasitised clutches, but parasitism can be an adaptive strategy if old females are parasitising the clutches of young ones (which lay earlier in the season) before incubating their own clutch.

Gang-brooding behaviour appears to be an adaptive strategy against chick predation, allowing parent hens to reduce their individual vigilance levels while increasing the corporate vigilance of the group. It is suggested that the small gang-brood sizes and the delay in onset serve to minimise the costs of amalgamation, such as adoption. Adoption does not appear to be an adaptive strategy, but a result of certain constraints of recognition. Playback experiments reveal that hens are probably susceptible to adoption at particular stages in their breeding cycle, when the costs of rejection outweigh the costs of accepting alien young.

The evidence therefore suggests that both nest parasitism and gang-brooding can be adaptive strategies, whereas dump nesting and adoption may be responses to particular constraints.

"Can I go now, Mum?"

REFERENCES

Abraham KF (1978) Adoption of spectacled eider ducklings by Arctic loons. *Condor* **80**: 289-340.

Afton AD (1984) Influence of age and time on reproductive performance of female lesser scaup. *Auk* **101**: 255-265.

Alexander RD & Borgia G (1979) On the origin and basis of the male-female phenomenon. *In: Blum MS & Blum NA (Eds): Sexual Selection and Reproductive Competition in Insects. Academic Press.*

Ali S & Ripley SD (1983) Handbook of the birds of India and Pakistan. Compact Edition. *OUP.*

Altmann SA, Wagner SS & Lennington S (1977) Two models for the evolution of polygyny. *Behav. Ecol. Sociobiol.* **2**: 397-410.

Anderson MG (1984) Parental investment and pair-bond behavior among canvasback ducks (*Aythya valisineria*, Anatidae). *Behav. Ecol. Sociobiol.* **15**: 81-90.

Andersson M (1978) Natural selection of offspring numbers: some possible intergenerational effects. *Amer. Natur.* **112**: 762-766.

Andersson M (1982a) Female choice selects for extreme tail length in a widowbird. *Nature* **299**: 818-820.

Andersson M (1982b) Sexual selection, natural selection and quality advertisement. *Biol. J. Linn. Soc.* **17**: 375-393.

Andersson M (1984) Brood parasitism within species. *In: Barnard CJ (Ed): "Producers and Scroungers: Strategies of Exploitation and Parasitism.*

Andersson M & Eriksson MOG (1982) Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *Amer. Natur.* **120**: 1-16.

Andersson M & Wiklund CG (1978) Clumping versus spacing out: experiments on nest predation in fieldfares (*Turdus pilaris*). *Anim. Behav.* **26**: 1207-1212.

Andersson M, Wiklund C & Rundgren H (1980) Parental defence of offspring: a model and an example. *Anim. Behav.* **28**: 536-542.

Ankney CD & MacInnes CD (1978) Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* **95**: 459-471.

Ar A & Yom-Tov Y (1978) The evolution of parental care in birds. *Evolution* **32**: 655-669.

Arak A (1984) Sneaky breeders. *In: Barnard CJ (Ed): Producers and Scroungers: Strategies of Exploitation and Parasitism.*

Armstrong EA (1956) Distraction display and the human predator. *Ibis* **98**: 641-654.

Arnold TW (1987) Conspecific egg discrimination in American coots. *Condor* **89**: 675-676.

Arnold TW, Rohwer FC & Armstrong T (1987) Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Amer. Natur.* **130**: 309-319.

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* **103**: 458-473.

Bagenal TB (1969) The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish. Biol.* **1**: 167-182.

Baillie SK & Milne H (1982) The influence of female age on breeding in the eider *Somateria mollissima. Bird Study* **29**: 55-66.

Baker ECS (1930) The game birds of India, Burma and Ceylon: Volume III. Pheasants and bustard quail. *Bombay Nat. Hist. Soc., London* .

Baker JMR (1990) Growth of larval and juvenile newts. *Ph.D. thesis, Open University, Milton Keynes.*

Baker JMR (1992) Ovum size and clutch size in smooth newts - no trade-off. *Unpub. manus.*

Barash DP (1975) Evolutionary aspects of parental behavior: distraction behavior of the Alpine accentor. *Wilson Bull.* **87**: 367-373.

Barash DP (1982) Sociobiology and behavior. *Elsevier, New York* .

Barnard CJ (1989) Kin recognition in vertebrates: introductory comments. *Ethol. Ecol. Evol.* **1**: 85-91.

Bateman AJ (1948) Intrasexual selection in *Drosophila. Heredity* **2**: 349-368.

Bayer RD (1982) How important are bird colonies as information centers? *Auk* **99**: 31-40.

Baylis JR (1981) The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Env. Biol. Fish.* **6**: 223-251.

Beard EB (1964) Duck brood behavior at the Seney National Wildlife Refuge. *J. Wildl. Management* **28**: 492-521.

Beasley K (1986) Feral Peafowl breeding at Monteith. *S. Austral. Ornithologist* **30**: 53.

Bédard J & Munro J (1976) Brood and crèche stability in the common eider of the S. Lawrence estuary. *Behaviour* **60**: 221-236.

Beebe W (1931) A monograph of the pheasants, Vol. IV. *Dover Press*: pp 161-190.

Beecher MD (1981) Development of parent-offspring recognition in birds. *In: Aslin RK, Alberts JR & Petersen MR (Eds): Development of perception, Vol 1. Academic Press, New York* : pp 45-66.

Beecher MD, Beecher IM, Lumpkin S & Hahn S (1981) Parent-offspring recognition in bank swallows (*Riparia riparia*). II. Development and acoustic basis. *Anim. Behav.* **29**: 95-101.

Beekman EM (Ed) (1988) Fugitive Dreams. An Anthology of Dutch Colonial Literature. *Univ. Massachusetts Pr., Amherst* .

Beer CG (1979) Vocal communication between laughing gull parents and chicks. *Behaviour* **70**: 118-146.

Begon M & Parker GA (1986) Should egg size and clutch size decrease with age? *Oikos* **47**: 293-302.

Behle WH (1958) The bird life of Great Salt Lake. *Univ. Utah Pr., Salt Lake City, Utah .*

Bekoff M (1975) Social behavior and ecology of African Canidae: a review. *In: Fox MW (Ed) The wild canids. Van Nostrand Reinhold, New York*: pp 120-142.

Bent AC (1964) Life histories of North American petrels and pelicans and their allies. *Dover Publications Inc., New York .*

Berglund A & Rosenqvist G (1986) Reproductive costs in the prawn *Palaemon adspersus*: effects on growth and predator vulnerability. *Oikos* **46**: 349-354.

Bergmann J (1980) The peafowl of the world. *Saiga Publ. Co. Ltd.*

Berry HH (1972) Flamingo breeding on the Etosha Pan, South West Africa, during 1971. *Madoqua Ser. I* : 5-31.

Bertram BCR (1975) Social factors influencing reproduction in wild lions. *J. Zool. Lond.* **177**: 463-482.

Bertram BCR (1976) Kin selection in lions and in evolution. *In: Bateson PG & Hinde RA (Eds) Growing points in ethology Cambridge Univ. Pr., Cambridge pp 281-301 .*

Bertram BCR (1978) Living in groups: predators and prey. *In: Krebs JR & Davies NB (Eds): Behavioural Ecology, an Evolutionary Approach. Blackwell, Oxford*: pp 64-96.

Bertram BCR (1979) Breeding system and strategies of ostriches. *Proc. XVII Int Ornith Congr .*

Bertram BCR (1980) Vigilance and group size in ostriches. *Anim. Behav.* **28**: 278-286.

Biermann GC & Robertson RJ (1981) An increase in parental investment during the breeding season. *Anim. Behav.* **29**: 487-489.

Birkhead TR, Burke T, Zann R, Hunter FM & Krupa AP (1990) Extra-pair paternity and intraspecific brood parasitism in wild zebra finches, *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* **27**: 315-324.

Birkhead TR & Møller AP (1992) Sperm competition in birds: evolutionary causes and consequences. *Academic Pr., London .*

Birkhead T & Møller A (1993) Female control of paternity. *Trends Ecol. Evol.* **8**: 100-104.

Black JM & Owen M (1986) Determinants of social rank in goose flocks; aquisition of social rank in young geese. *Z. Tierpsychol.* : 129-145 (or 1989 - see p 183; also need vol. no.; also check title)

Black JM & Owen M (1989a) Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Anim. Behav.* **37**: 199-209.

Black JM & Owen M (1989b) Parent-offspring relationships in wintering barnacle geese. *Anim. Behav.* **37**: 187-198.

Blancher PJ & Robertson RJ (1982) Kingbird aggression: does in deter predation? *Anim. Behav.* **30**: 929-930.

Blumer LS (1979) Male parental care in the bony fishes. *Q. Rev. Biol.* **54**: 149-161.

Boersma PD (1982) Why some birds take so long to hatch. *Am. Nat.* **120**: 733-750.

Boersma PD (1991) Asynchronous hatching and food allocation in the Magellanic penguin *Spheniscus magellanicus. Acta XX Int. Ornith. Congr*: pp 962-973.

Boersma PD & Stokes DL (1991) Asynchronous hatching and growth of magellanic penguin chicks: who's in control? *Acta XX Int. Ornith. Congr*: pp 273-274.

Boness DJ (1990) Fostering behaviour in Hawaiian Monk Seals: is there a reproductive cost? *Behav. Ecol. Sociobiol.* **27**: 113-122.

Boos JD, Nudds TD & Sjoberg K (1989) Posthatch brood amalgamation by mallards. *Wilson Bull.* **101**: 503-505.

Boucher DH (1977) On wasting parental investment. *Amer. Natur.* **111**: 786-788.

Breitwisch R (1989) Mortality patterns, sex ratios, and parental investment in monogamous birds. *In: Power DM (Ed): Curr. Ornith. Vol. 6. Plenum Press, NY & London*: pp 1-50.

Bright M (1993) The private life of birds: a worldwide exploration of bird behaviour. *Bantam Press, London.*

Brooke M de L (1978) Sexual differences in the voice and individual vocal recognition in the Manx shearwater (*Puffinus puffinus*). *Anim. Behav.* **26**: 622-629.

Brooke M & Birkhead T (Eds) (1991) The Cambridge encyclopedia of ornithology. *Cambridge University Press.*

Broom DM (1981) Biology of behaviour. *Cambridge Univ. Pr., Cambridge.*

Brosset A (1962) The bats of central and western India (Part 2). *J. Bombay Nat. Hist. Soc.* **59**: 583-624.

Brown CR (1984) Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. *Science* **224**: 518-519.

Brown CR & Brown MB (1989) Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. *Anim. Behav.* **37**: 777-796.

Brown CR & Brown MB (1991) Selection of high quality host nests by parasitic cliff swallows. *Anim. Behav.* **41**: 457-466.

Brown JL (1978) Avian communal breeding systems. *Ann. Rev. Ecol. Syst.* **9**: 123-155.

Brown JL (1987) Helping and communal breeding in birds. *Princeton Univ. Pr., Princeton, N.J.*

Brown JL, Brown ER, Brown SD & Dow DD (1982) Helpers: effects of experimental removal on reproductive success. *Science* **215**: 421-422.

Brown JL, Dow DD, Brown ER & Brown SD (1978) Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behav. Ecol. Sociobiol.* **4**: 43-59.

Brown LH (1958) The breeding of the greater flamingo *Phoeniconaias ruber* at Lake Elmenteita, Kenya Colony. *Ibis* **100**: 388-420.

Brown LH & Root A (1971) The breeding behaviour of the lesser flamingo *Phoeniconaias minor. Ibis* **113**: 147-172.

Brown LH & Urban EL (1969) The breeding biology of the great white pelican *Pelecanus onocrotalus roseus* at Lake Shala, Ethopia. *Ibis* **111**: 199-237.

Brunton DH (1986) Fatal antipredator behavior by killdeer. *Wilson Bull.* **98**: 605-607.

Brunton DH (1990) The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian parental defense. *Behav. Ecol. Sociobiol.* **26**: 181-190.

Burger J & Gochfeld M (1992) Effect of group size on vigilance while drinking in the coati, *Nasua narica*, in Costa Rica. *Anim. Behav.* **44**: 1053

Burley N (1977) Parental investment, mate choice, and mate quality. *Proc. Nat. Acad. Sci. USA* **74**: 3476-3479.

Burley N (1986) Sex ratio manipulation in color-banded populations of zebra finches. *Evolution* **40**: 1191-1206.

Burtt EH Jr (1977) Some factors in the timing of parent-chick recognition in swallows. *Anim. Behav.* **25**: 231-239.

Byers JA & Bekoff M (1986) What does kin recognition mean? *Ethology* **72**: 342-345.

Capinera JL (1979) Qualitative variation in plants and insects: effect of propagule size on ecological plasticity. *Am. Nat.* **114**: 350-361.

Caraco T, Martindale S & Pulliam HR (1980) Avian time budgets and distance to cover. *Auk* **97**: 872-875.

Carey C, Rahn H & Parisi P (1980) Calories, lipid, water and yolk in avian eggs. *Condor* **82**: 335-343.

Carlisle TR (1985) Parental response to brood size in a cichlid fish. *Anim. Behav.* **33**: 234-238.

Caro TM (1987) Cheetah mothers' vigilance; looking out for prey or for predators? *Behav. Ecol. Sociobiol.* **20**: 351-361

Carr N (1965) Return to the wild. *Fontana Books, London.*

Carrick R (1964) Breeding biology of *Eudyptes. In: Thomson AL (Ed) A new dictionary of birds. Nelson, London:* p 614.

Carter HR & Hobson KA (1988) Creching behavior of Brandt's cormorant chicks. *Condor* **90**: 395-400.

Charnov EL (1981) Kin selection and helpers at the nest: effects of paternity and biparental care. *Anim. Behav.* **29**: 631-632.

Choudhury S, Jones CS, Black JM & Prop J (1993) Adoption of young and intraspecific nest parasitism in barnacle geese. *Condor* **95**: 860-868.

Christensen GC (1954) The chukar partridge in Nevada. *Nevada Fish and Game Comm., Reno; Biol. Bull.* **1**: 1-77.

Clutton-Brock TH (1984) Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* **123**: 212-229.

Clutton-Brock TH (1988) Reproductive success. *In: Clutton-Brock TH (Ed): Reproductive Success: Studies of individual variation in contrasting breeding systems. Univ. Chicago Press*: pp 472-485.

Clutton-Brock TH (1989) Mammalian mating systems. *Proc. Roy. Soc. B* **235**: 339-372.

Clutton-Brock TH (1991) The evolution of parental care. *Princeton Univ. Press, Princeton, N.J.*

Clutton-Brock TH, Albon SD & Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* **308**: 358-360.

Clutton-Brock TH, Guinness FE & Albon SD (1982) Red deer: the behaviour and ecology of two sexes. *Univ. Chicago Pr., Chicago.*

Clutton-Brock TH & Parker GA (1992) Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* **67**: 437-456.

Clutton-Brock TH & Vincent ACJ (1991) Sexual selection and the potential reproductive rates of males and females. *Nature* **351**: 58-60.

Cody ML (1971) Ecological aspects of reproduction. *In: Farner DS & King JR (Eds) Avian biology, Volume I. Academic Pr*: pp 461-512.

Coleman RM & Fischer RU (1991) Brood size, male fanning effort and the energetics of a nonshareable parental investment in bluegill sunfish, *Lepomis macrochirus* (Teleostei: Centrarchidae) *Ethology* **87**: 177-188

Colgan P (1983) Comparative Social Recognition. *Wiley, New York.*

Cooch EG, Lank DB, Dzubin A, Rockwell RF & Cooke F (1991) Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* **72**: 503-512.

Coulson JC (1963) Egg size and shape in the kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proc. Zool. Soc. Lond.* **140**: 211-227.

Coulson JC (1966) The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla. J. Anim. Acol.* **35**: 269-279.

Crivelli A (1981) The dalmation pelican, *Pelecanus crispus* Bruch 1832, a recently world-endangered species. *Biol Conserv.* **20**: 297-310.

Croxall JP (1982) Energy costs of incubation and moult in petrels and penguins. *J. Anim. Ecol.* **51**: 171-194.

Crump ML (1981) Variation in propagule size as a function of environmental uncertainty for tree frogs. *Am. Nat.* **117**: 724-737.

Cullen E (1957) Adaptations in the kittiwake to cliff nesting. *Ibis* **99**: 275-302.

Curio EB (1978) The adaptive significance of avian mobbing. *Z. Tierpsychol.* **48**:175-183

Curio E (1983) Why do young birds reproduce less well?. *Ibis* **125**: 400-404.

Curio E (1987) Animal decision-making and the Concorde fallacy. *Trends Ecol. Evol.* **6**: 1458-1462.

Curio E (1988) Relative realized lifespan and delayed cost of parental care. *Am. Nat.* **131**: 825-836.

Curio E, Regelmann K & Zimmerman U (1984) The defence of first and second broods by great tit (*Parus major*) parents: a test of predictive sociobiology. *Z. Tierpsychol.* **66**: 101-127.

Dagg A & Foster J (1976) The giraffe: its biology, behavior, and ecology. *Van Nostrand Reinhold, New York.*

Dahlgren J (1990) Females choose vigilant males: an experiment with the monogamous grey partridge, *Perdix perdix.* Anim. Behav. **39**: 646-651.

Darwin C (1871) The descent of man and selection in relation to sex. *John Murray, London.*

Davies SJJF & Carrick R (1962) On the ability of crested terns, *Sterna bergii*, to recognise their own chicks. *Austral. J. Zool.* **10**: 171-177.

Davis LS (1982a) Crèching behaviour of Adelie penguin chicks (*Pygoscelis adeliae*). *N.Z. J. Zool.* **9**: 279-286.

Davis LS (1982b) Timing of nest relief and its effect on breeding success in Adelie penguins (*Pygoscelis adeliae*). *Condor* **84**: 178-183.

Davis LS (1988) Coordination of incubation routines and mate choice in Adelie penguins (*Pygoscelis adeliae*). *Auk* **105**: 428-432.

Davis RB, Herreid CF II & Short HL (1962) Mexican free-tailed bats in Texas. *Ecol. Monogr.* **32**: 311-346.

Dawkins R (1976) The selfish gene. *Oxford Univ. Pr., Oxford.*

Dawkins R & Carlisle TR (1976) Parental investment, mate desertion and a fallacy. *Nature* **262**: 131-133.

Dawkins R & Krebs JR (1978) Arms races between and within species. *Proc. Roy. Soc. Lond. B* **205**: 489-511.

de Clinchamp T (1982) Somptueux paons blancs. *J. des Oiseaux* **157**: 33.

Deag J & Crook JH (1971) Social behaviour and "agonistic buffering" in the wild Barbary macaque, *Macaca sylvana. Folia Primatol.* **15**: 183-280.

Deeming DC (1991) Reasons for the dichotomy in egg turning in birds and reptiles. *In: Deeming DC & Ferguson MWJ (Eds) Egg incubation: its effects on embryonic development in birds and reptiles. Cambridge Univ. Pr.:* pp 307-323.

de Groot P (1980) Information transfer in a socially roosting weaver bird (*Quelea quelea*: Ploceinae): an experimental study. *Anim. Behav.* **28**: 1249-1254.

Dehn MM (1990) Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**: 337-342.

Delacour J (1977) The Pheasants of the world (2nd edition). *Spur Publications in conjunction with the WPA.*

Dick JTA & Elwood RW (1993) The mating system of *Gammarus pulex*: a negligable role for micro-habitat segregation. *Anim. Behav.* **45**: 188-190.

Dilger WC & Wallen JC (1966) The pecking responses of peafowl chicks. *The Living Bird* **5**: 115-125.

Dimond S & Lazarus J (1974) The problem of vigilance in animal life. *Brain Behav. Evol.* **9**: 60-79.

Drent RH & Daan S (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225-253.

Dunford C (1977) Behavioral limitation of round-tailed ground squirrel density. *Ecology* **58**: 1254-1268.

Eadie JM (1991) Constraint and opportunity in the evolution of brood parasitism in waterfowl. *Acta XX Congress. Internat. Ornithol.* **XX**: 1031-1041.

Eadie JM, Kehoe FP & Nudds TD (1988) Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Can. J. Zool.* **66**: 1709-1721.

Eadie TMcA & Lumsden HG (1985) Is nest parasitism always deleterious to goldeneyes? *Amer. Natur.* **126**: 859-866.

Eisner E (1960) The relationship of hormones to the reproductive behaviour of birds, referring especially to parental behaviour: a review. *Anim. Behav.* **8**: 155-179.

Elwood RW & Dick JTA (1990) The amorous Gammarus: the relationship between precopula duration and size-assortative mating in *Gammarus pulex*. *Anim. Behav.* **39**: 828-833.

Emlen JT Jr (1941) An experimental analysis of the breeding cycle of the tricolored redwing. *Condor* **43**: 209-219.

Emlen JT (1970) Age specificity and ecological theory. *Ecology* **51**: 588-601.

Emlen ST (1978) The evolution of cooperative breeding in birds. *In: Krebs JR & Davies NB (Eds): Behavioural Ecology, an Evolutionary Approach. Blackwell, Oxford:* pp 245-281.

Emlen ST (1981) Altruism, kinship and reciprocity in the white-fronted bee-eater. *In: Alexander RD & Tinkle D (Eds) Natural selection and social behaviour. Chiron Press, NY:* pp 217-230 .

Emlen ST (1984) Cooperative breeding in birds and mammals. *In: Krebs JR & Davies NB (Eds): Behavioural Ecology, an Evolutionary Approach. Blackwell, Oxford:* pp 305-339 .

Emlen ST (1992) Evolution of cooperative breeding in birds and mammals. *In: :* pp 301-337.

Erkmann WJ (1983) The evolution of polyandry in shorebirds: an evaluation of hypotheses. *In: Wasser SK (Ed) Social behaviour of female vertebrates. Academic Pr. NY:* pp 113-168 .

Evans PGH (1988) Intraspecific nest parasitism in the European starling *Sturnus vulgaris*. *Anim. Behav.* **36**: 1282-1294.

Evans RM (1970a) Imprinting and the control of mobility in ring-billed gulls (*Larus delawarensis*). *Anim. Behav. Monogr.* **3**: 193-248.

Evans RM (1970b) Parental recognition and the 'mew call' in black-billed gulls (*Larus bulleri*). *Auk* **87**: 503-513.

Evans RM (1980a) Development of behavior in seabirds: an ecological perspective. *In: Burger J, Olla BL & Winn HE (Eds) Plenum Publ. Corp., New York:* pp 271-322.

Evans RM (1980b) Development of individual call recognition in young ring-billed gulls (*Larus delawarensis*): an effect of feeding. *Anim. Behav.* **28**: 60-67.

Evans RM (1984a) Development of thermoregulation in young white pelicans. *Can. J. Zool.* **62**: 808-813.

Evans RM (1984b) Some causal and functional correlates of creching in young white pelicans. *Can. J. Zool.* **62**: 814-819.

Evans RM (1990) The relationship between parental input and investment. *Anim. Behav.* **39**: 797-798.

Evans RM & Lee SC (1991) Terminal-egg neglect: brood reduction strategy or cost of asynchronous hatching? *Acta XX Int. Ornith. Congr.* 1734-1740.

Ewer RF (1973) The carnivores. *Weidenfeld & Nicolson, London.*

Fagen RBL (1972) An optimal life history strategy in which reproductive effort decreases with age. *Amer. Natur.* **106**: 258-261.

Falls JB (1982) Individual recognition by sounds in birds. *In: Kroodsma DH & Miller EH (Eds): Acoustic Communication in Birds, Vol 2. Academic Press, New York:* pp 237-278.

Fisher RA (1930) The genetical theory of natural selection. *Oxford Univ. Pr., Oxford.*

Fitzgibbon CD (1989) A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.* **37**: 508-510.

Fleischer RC (1985) A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behav. Ecol. Sociobiol.* **17**: 91-99.

Fogden SCL (1971) Mother-young behaviour at grey seal breeding beaches. *J. Zool.* **164**: 61-92.

Forslund P (1993) Vigilance in relation to brood size and predator abundance in the barnacle goose *Branta leucopsis. Anim. Behav.* **45**: 965-973.

Fraser DF (1980) On the environmental control of oocyte maturation in a plethodontid salamander. *Oecologia* **46**: 302-307.

Friedman H (1963) Host relations of the parasitic cowbirds. *U.S. Nat. Mus. Bull.* **223**: 1-196.

Fujioka M (1985) Sibling competition and siblicide in asynchronously hatching broods of the cattle egret *Bubulcus ibis. Anim. Behav.* **33**: 1218-1242.

Gaston AJ (1975) Methods for estimating bird populations. *J. Bombay Nat. Hist. Soc.* **72**: 271-283.

Gittleman JL (1985) Functions of communal care in mammals. *In: Greenwood PJ, Harvey PH & Slatkin M (Eds) Evolution: essays in honour of John Maynard Smith. Cambridge Univ. Pr., Cambridge:* pp 181-205 .

Goldsmith O (1774) A history of the earth and animated nature (Book IV).

Gorman ML & Milne H (1972) Creche behaviour in the common eider *Somateria m. mollissima* L. *Ornis Scandinavica* **3**: 21-25.

Gosling LM (1969) Parturition and related behaviour in Coke's hartebeest, *Alcelaphus buselaphus cokei* Günther. *J. Reprod. Fert. Suppl.* **6**: 265-286.

Gosling LM (1986a) Biased sex ratios in stressed animals. *Amer. Natur.* **127**: 893-896.

Gosling LM (1986b) Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality. *Amer. Natur.* **127**: 772-795.

Gottlieb G (1965a) Components of recognition in ducklings. *In: Topoff H (Ed) Nat. Hist., Ch. 21* **74**: 12-19.

Gottlieb G (1965b) Imprinting in relation to parental and species identification by avian neonates. *J. Comp. Physiol. Psychol.* **59**: 345-356.

Gottlieb G (1971) Development of species identification in birds. *Univ. Chicago Press.*

Grafen A (1980) Opportunity cost, benefit and degree of relatedness. *Anim. Behav.* **28**: 967-968.

Grant MC (1991) Relationships between egg size, chick size at hatching, and chick survival in the whimbrel *Numenius phaeopus. Ibis* **133**: 127-133.

Graves JA & Whiten A (1980) Adoption of strange chicks by herring gulls, *Larus argentatus* L. *Z. Tierpsychol.* **54**: 267-278.

Greig-Smith PW (1980) Parental investment in nest defence by Stonechats (*Saxicola torquata*). *Anim. Behav.* **28**: 604-619.

Grice D & Rodgers JP (1965) The wood duck in Massachusetts. *Final report, Federal Aid-in-Wildlife Restoration Project No. W-19-R Massachusetts Division of Fisheries and Game, Westboro, Massachusetts.*

Gross AO (1938) Eider ducks of Kent Island. *Auk* **55**: 387-400.

Gross MR & Sargent RC (1985) The evolution of male and female parental care in fishes. *Am. Zool.* **25**: 807-822.

Gubernick DJ (1980) Maternal "imprinting" or maternal "labelling" in goats? *Anim. Behav.* **28**: 124-129.

Gubernick DJ (1981) Parent and infant attachment in mammals. *In: Gubernick EJ & Klopfer PH (Eds) Parental care in mammals. Plenum Pr., New York:* pp 243-305.

Gustin MK & McCracken GF (1987) Scent recognition in the Mexican free-tailed bat, *Tadarida brasiliensis mexicana. Anim. Behav.* **35**: 13-19.

Hafez ED, Sumption LJ & Jackway JS (1962) The behavior of swine. *In: Hafez ES (Ed) The behavior of domestic animals. Williams and Wilkins, Baltimore:* pp 334-369.

Hahn DC (1981) Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. *Anim. Behav.* **29**: 421-427.

Hamilton WD (1964) The genetical evolution of social behaviour. I. *J. Theoret. Biol.* **7**: 1-16.

Hamilton WD (1971) Geometry for the selfish herd. *J. Theoret. Biol.* **31**: 295-311.

Hamilton WJ & Orians GH (1965) Evolution of brood parasitism in altricial birds. *Condor* **67**: 361-382.

Hamann J & Cooke F (1989) Intra-seasonal decline of clutch size in lesser snow geese. *Oecologia* **79**: 83-90.

Harvey PH & Clutton-Brock TH (1989) Life history variation in primates. *Evolution* **39**: 559-581.

Harvey PH & Greenwood PJ (1978) Anti-predator defence strategies: some evolutionary problems. *In: Krebs JR & Davies NB (Eds): Behavioural Ecology, an Evolutionary Approach. Blackwell, Oxford.*

Harvey PH, Read AF & Promislow DEL (1989) Life history variation in placental mammals: unifying data with theory. *Oxford Surveys in Evolutionary Biology* **6**: 13-31.

Hébert PN (1988) Adoption behaviour by gulls: a new hypothesis. *Ibis* **130**: 216-220.

Heinroth O (1911) Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Acta V Int. Ornith. Congr., Berlin:* pp 333-342.

Hersher L, Richmond JB & Moore AV (1963) Maternal behavior in sheep and goats. *In: Rheingold HL (Ed) Maternal behavior in mammals. Wiley, New York:* pp 203-232.

Hess EH (1959) Imprinting. *Science* **130**: 133-141.

Hess EH (1973) Imprinting: early experience and the developmental psychobiology of attachment. *Van Nostrand Reinhold, New York .*

Hess EH & Petrovich S (Eds) (1977) Imprinting. *Dowden, Hutchinson & Ross, Stroudsberg.*

Heusmann HW, Bellville R & Burrell RG (1980) Further observations on dump nesting by wood ducks. *J. Wildl. Manage.* **44**: 908-915.

Hillgarth N (1984) Social organisation of wild peafowl in India. *WPA Journal* **9**: 47-56.

Hinton HE (1981) Biology of insect eggs. *Pergamon Pr., Oxford.*

Hirshfield MF & Tinkle DW (1975) Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci. USA* **72**: 2227-2231.

Holley AJF (1981) Naturally arising adoptions in the herring gull. *Anim. Behav.* **29**: 302-303.

Holley AJF (1984) Adoption, parent-chick recognition and maladaption in the herring gull, *Larus argentatus. Z. Tierpsychol.* **64**: 9-14.

Hori J (1964) Parental care in the shelduck. *Wildfowl* **15**: 100-103.

Howard RD (1978) The evolution of mating strategies in bullfrogs, *Rana catesbiana. Evolution* **32**: 850-871.

Hrdy SB (1976) Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *In: Rosenblatt J, Hinde R, Shaw E & Bier C (Eds) Advances in the study of behavior, Volume 6. Academic Press, New York:* pp 101-158.

Hrdy SB (1977) The langurs of Abu. *Harvard Univ. Pr., Cambridge, USA* .

Hudson PJ & Newborn D (1990) Brood defence in a precocial species: variations in the distraction displays of red grouse, *Lagopus lagopus scoticus. Anim. Behav.* **40**: 254-261.

Humphries DA & Driver PM (1967) Erratic display as a defense against predators. *Science* **156**: 1767-1768.

Inglis IR & Lazarus J (1981) Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.* **57**: 193-200.

Itani J (1959) Paternal care in the wild Japanese monkey, *Macaca juscata fuscata. Primates* **2**: 61-93.

Jay P (1962) Aspects of maternal behavior among langurs. *Ann. N.Y. Acad. Sci.* **102**: 468-476.

Jennings T & Evans SM (1980) Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris. Anim. Behav.* **28**: 634-635.

Jerdon TC (1864) Birds of India, Volume 3. *Wyman, Calcutta, India.*

Johnsgard PA (1986) Pheasants of the world. *OUP* .

Johnsingh AJT & Murali S (1978) The ecology and behaviour of the Indian Peafowl (*Pavo cristatus*) Linn. of Injar. *J. Bombay Nat. Hist. Soc.* **75**: 1069-1079.

Jones DN (1991) Sexual conflict in a promiscuous megapode (oral contributed paper). *Acta XX Int. Ornith. Congr:* 407.

Jouventin P (1982) Visual and vocal signals in penguins, their evolution and adaptive characters. *Verlag, Berlin.*

Kahl MP (1970) East Africa's majestic flamingoes. *Nat. Geog. Mag.* **137**: 276-294.

Kear J (1970) The adaptive radiation of parental care in waterfowl. *In: Crook JH (Ed) Social Behaviour in Birds and Mammals. Acad. Press Lond/NY:* pp 357-392.

Kehoe FP (1986) The adaptive significance of crèching behavior in the white-winged scoter (*Melanitta fusca deglendi*). *M.Sc. thesis, Univ. of Guelph, Guelph, Ontario (cited in Eadie et al. 1988)* .

Kehoe FP (1989) The adaptive significance of crèching behaviour in the white-winged scoter (*Melanitta fusca deglandi*). *Can. J. Zool.* **67**: 406-411.

Kendeigh SC (1952) Parental care and its evolution in birds. *Illinois Biological Monogr. XXII No's 1-3. Univ. Illinois Press, Urbana.*

Kennedy ED, Stouffer PC & Power HW (1989) Post-ovulatory follicles as a measure of clutch size and brood parasitism in European starlings. *Condor* **91**: 471-473.

Keys GC & Dugatkin LA (1990) Flock size and position effects on vigilance, aggression, and prey capture in the European starling. *The Condor* **92**: 151-159

King JR (1973) Energetics of reproduction in birds. *In: Farner DS (Ed) Breeding biology of birds. Nat. Acad. Sci., Washington D.C:* pp78-107.

King WB (Ed) (1981) Endangered birds of the world: the I.C.B.P. red data book. *International Council for Bird Preservation.*

Kirkham V (1991) Chapter Three: the poisoned peacock. *Manuscript:* pp 1-93.

Kleiman DG (1985) Paternal care in New World primates. *Amer. Zool.* : 857-859.

Kleiman DG & Malcolm JR (1981) The evolution of male parental investment in mammals. *In: Gubernick DJ & Klopfer PH (Eds) Parental care in mammals Plenum Pr., NY:* pp 347-387.

Klomp H (1970) The determination of clutch-size in birds: a review. *Ardea* **58**: 1-122.

Klopfer PH & Klopfer MS (1968) Maternal imprinting in goats: fostering of alien young. *Z. Tierpsychol.* **25**: 862-866.

Knapton RW (1984) Parental investment: The problem of currency. *Can. J. Zool.* **62**: 2673-2674.

Knight RL & Temple SA (1986) Why does intensity of avian nest defense increase during the nesting cycle? *Auk* **103**: 318-327.

Knight RL & Temple SA (1988) Nest-defense behaviour in the red-winged blackbird. *Condor* **90**: 193-200.

Knudsen B & Evans RM (1986) Parent-young recognition in herring gulls (*Larus argentatus*). *Anim. Behav.* **34**: 77-80.

Krebs JR, MacRoberts MH & Cullen JM (1972) Flocking and feeding in the great tit *Parus major* - an experimental study. *Ibis* **114**: 507-530.

Krebs JR & Davies NB (1987) An introduction to behavioural ecology (2nd edition). *Blackwell Scientific Publications.*

Kuck TL, Dahlgren RB & Progulske DR (1970) Movements and behaviour of hen pheasants during the nesting season. *J. Wildl. Mgmt.* **34**: 626-630.

Kummer H (1968) Social organization of Hamadryas baboons: a field study. *Univ. Chicago Pr., Chicago.*

Lack D (1947) The significance of clutch size. *Ibis* **89**: 302-352.

Lack D (1954) The natural regulation of animal numbers. *Clarendon Press, Oxford.*

Lack D (1966) Population studies of birds. *Clarendon Press, Oxford.*

Lack D (1968) Ecological adaptations for breeding in birds. *Methuen, London.*

Lancaster J (1971) Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecuc aethiops*). *Folia Primatol.* **15**: 161-182.

Laws RM & Clough G (1966) Observations on reproduction in the hippopotamus *Hippopotamus amphibius* Linn. *Symp. Zool. Soc. Lond.* **15**: 117-140.

Lazarus J (1972) Natural selection and the function of flocking in birds: a reply to Murton. *Ibis* **114**: 556-558.

Lazarus J (1978) Vigilance, flock size and domain of danger size in the white-fronted goose. *Wildfowl* **29**: 135-145.

Lazarus J (1979) Flock size and behaviour in captive red-billed weaver birds (*Quelea quelea*): implications for social facilitation and the functions of flocking. *Behaviour* **71**: 127-145.

Lazarus J (1990) Looking for trouble. *New Scientist, 27th Jan:* pp 62-65.

Lazarus J & Inglis IR (1978) The breeding behaviour of the pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour* **65**: 62-87.

Lazarus J & Inglis IR (1986) Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim.Behav.* **34**: 1791-1804.

Lazarus J & Symonds M (1992) Contrasting effects of protective and obstructive cover on avian vigilance. *Anim. Behav.* **43**: 519-528.

Lendrem DW (1982) Vigilance in birds. *DPhil Thesis, Oxford.*

Lessells CM (1986) Brood size in Canada geese - a manipulation experiment. *J. Anim. Ecol.* **55**: 669-689.

Lessells CM (1987) Parental investment, brood size and time budgets: behaviour of lesser snow goose families. *Ardea* **75**: 189-203.

Lima LL & Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619-641.

Linden M & Møller AP (1989) Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* **4**: 367-370.

Lloyd DG (1984) Variation strategies of plants in heterogeneous environments. *Biol. J. Linn. Soc.* **21**: 357-385.

Lloyd DG (1987) Selection of offspring size at independence and other size-versus-number strategies. *Amer. Natur.* **129**: 800-817.

Lorenz K (1935) Der Kumpan in der Umvelt des Vögels. *J. Ornithol.* **83**: 213.

Lott DF (1972) The way of the bison: fighting to dominance. *In: Marler PR (Ed) The marvels of animals behavior. Nat. Geog. Soc., Washington DC:* pp 321-332.

Low BS (1978) Environmental uncertainty and the parental strategies of marsupials and placentals. *Amer. Natur.* **112**: 197-213.

Lyon BE (1991) Brood parasitism in American coots: avoiding the constraints of parental care. *Acta xx Con. Int. Orn*: 1023-1030.

Lyon BE (1993) Conspecific brood parasitism as a flexible female reproductive tactic in American coots. *Anim. Behav.* **46**: 911-928.

Mackie RJ & Buechner HK (1963) The reproductive cycle of the chukar. *J. Wildl. Management.* **27**: 246-260.

Mackworth JF (1970) Vigilance and attention: a signal detection approach. *Penguin Books, Harmondsworth.*

Magrath RD (1992) Seasonal changes in egg-mass within and among clutches of birds: general explanations and a field study of the blackbird *Turdus merula. Ibis* **134**: 171-179.

Manning JT (1985) Choosy females and correlates of male age. *J. Theoret. Biol.* **116**: 349-354.

Manning JT (1987) The Peacock's train and the age-dependency model of female choice. *WPA Journal* **12**: 44-56.

Manning JT (1989) Age-advertisement and the evolution of the peacock's train. *J. Evol. Biol.* **2**: 379-384.

Martin P & Bateson P (1986) Measuring behaviour: an introductory guide. *Cambridge Univ. Pr., Cambridge .*

May RM, Nee S, Watts C (1991) Could intraspecific brood parasitism cause population cycles? *Acta xx Con. Int. Orn.:* 1012-1021.

Maynard Smith J (1977) Parental investment: a prospective analysis [Niko Tinbergen Lecture 1976]. *Anim. Behav.* **25**: 1-9.

Maynard Smith J (1982) Evolution and the theory of games. *Cambridge Univ. Pr., Cambridge.*

Maynard Smith J (1984) The ecology of sex. *In: Krebs JR & Davies NB (eds). Behavioural Ecology: an evolutionary approach. Blackwell, Oxford:* pp 201-221.

McFarland D (1981) The Oxford companion to animal behaviour. *Oxford University Press, Oxford (reprinted with corrections 1987).*

McGillivray W (1923) The nesting of the Australian pelican *P. conspicullatus. Emu* **22**: 162-174.

McGinley MA (1989) The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol. Ecol.* **3**: 150-156.

McGinley MA & Charnov EL (1988) Multiple resources and the optimal balance between size and number of offspring. *Evol. Ecol.* **2**: 77-84.

McKaye KR & McKaye NM (1977) Communal care and kidnapping of young by parental cichlids. *Evolution* **31**: 674-681.

McKenna J (1981) Primate infant caregiving behavior. *In: Gubernick DJ & Klopfer PH (Eds) Parental care in mammals. Plenum Press, NY.*

McNamara JM & Houston AI (1992) Evolutionarily stable levels of vigilance as a function of group size: *Maevia inclemens*, dimorphic morph-independent mate selection in. *Anim. Behav.* **43**: 247- (check ref)

Medvin MB & Beecher MD (1986) Parent-offspring recognition in the barn swallow (*Hirundo rustica*). *Anim. Behav.* **34**: 1627-1639.

Middleton ALA (1977) Effect of cowbird parasitism on American goldfinch nesting. *Auk* **94**: 304-307.

Mills JA (1973) The infuence of age and pair-bond on the breeding biology of the red-billed gull *Larus novaehollandiae scopulinus. J. Anim. Ecol.* **42**: 147-162.

Milonoff M (1989) Can nest predation limit clutch size in precocial birds? *Oikos* **55**: 424-427.

Mock DW (1984) Siblicidal aggression and resource monopolization in birds. *Science* **225**: 731-733.

Mock DW & Ploger BJ (1987) Parental manipulation of optimal hatch asynchrony in cattle egrets: an experimental study. *Anim. Behav.* **35**: 150-160.

Møller AP (1987) Intraspecific nest parasitism and anti-parasite behaviour in swallows. *Anim. Behav.* **35**: 247-254.

Møller AP & Petrie M (1991) Evolution of intraspecific variability in birds' eggs: is intraspecific nest parasitism the selective agent?. *Acta XX Cong. Int. Orn.:* 1041-1048.

Montgomerie RD & Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**: 167-187.

Morris D (1957) Courtship of pheasants. *Zoo Life* **12**: 8-13.

Morse DH (1970) Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* **40**: 119-168.

Mukherjee AJ (1979) Peacock - our national bird. *Ministry of Information and Broadcasting, Gov't of India, New Delhi.*

Munro J (1975) L'élevage des jeunes chez l'eider commun (*Somateria mollissima*) dans l'estuaire du Saint-Laurent. *M.Sc. thesis, Université Laval, Québec.*

Munro J & Bédard J (1977a) Crèche formation in the common eider. *Auk* **94**: 759-771.

Munro J & Bédard J (1977b) Gull predation and crèching behaviour in the common eider. *Anim. Ecol.* **46**: 799-810.

Murton RK & Westwood NJ (1977) Avian breeding cycles. *Clarendon Pr., Oxford.*

Murton RK, Westwood NJ & Isaacson AJ (1974) Factors affecting egg-weight, body-weight and moult of the woodpigeon *Columba palumbus. Ibis* **116**: 52-73.

Nastase AJ (1983) Behavioral ecology of the Canada goose *Branta canadensis. Ph.D. thesis, Univ. of Pittsburgh, Pittsburgh, PA (cited in Eadie et al. 1988)*.

Navaneethakannan K (1984) Activity patterns in a colony of peafowls (*Pavo cristatus*) in nature. *J. Bombay Nat. Hist. Soc.* **81**: 387-393.

Neal E (1970) The banded mongoose, *Mungos mungo* Gmelin. *E. Afr. Wildl. J.* **8**: 63-71.

Nelson JB (1966) The breeding biology of the gannet *Sula bassana* on the Bass Rock, Scotland. *Ibis* **108**: 584-626.

Newton I, Marquiss M & Moss D (1981) Age and breeding in sparrowhawks. *J. Anim. Ecol.* **50**: 839-853.

Nice MM (1962) Development of behavior in precocial birds. *Trans. Linn. Soc. N.Y.* **8**: 1-211.

Nisbet ICT (1973) Courtship feeding, egg size and breeding success in common terns. *Nature* **241**: 141-142.

Nisbet ICT (1977) Courtship feeding and clutch size in common terns, *Sterna hirundo. In: Stonehouse BM & Perrins CM (Eds) Evolutionary ecology. University Park Press, Baltimore:* pp 101-109.

Nudds TD (1980) Canvasback tolerance of redhead parasitism: an observation and an hypothesis. *Wilson Bull.* **92**: 414.

Nur N (1983) On parental investment during the breeding season. *Anim. Behav.* **31**: 309-311.

Oates N (1898) Fauna of British India (Birds), Volume IV. *Taylor & Franchais, London.*

O'Connor RJ (1978) Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim. Behav.* **26**: 79-96.

O'Connor R (1984) The growth and development of birds. *Wiley, Chichester, England.*

Onnebrink H & Curio E (1991) Brood defense and age of young: a test of the vulnerability hypothesis. *Behav. Ecol. Sociobiol.* **29**: 61-68.

Packer CR (1980) Male care and exploitation of infants in *Papio anubis. Anim. Behav.* **28**: 512-520.

Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ & Mulder MB (1988) Reproductive success of lions. *In: Clutton-Brock TH (Ed): Reproductive Success. Univ. Chicago Press*: pp 363-383.

Packer CR & Pusey AE (1984) Infanticide in carnivores. *In: Hausfater G & Hrdy SB (Eds) Infanticide in animals and man: comparative and evolutionary perspcctivcs. Aldine, New York:* pp 31-42.

Parker GA (1974) Courtship persistence and female-guarding as male time investment strategies. *Behaviour* **28**: 512-520.

Parsons J (1970) Relationship between egg size and post-hatching chick mortality in the herring gull (*Larus argentatus*). *Nature* **228**: 1221-1222.

Parsons J (1975) Asynchronous hatching and chick mortality in the herring gull *Larus argentatus. Ibis* **117**: 517-520.

Parsons J (1976) Factors determining the number and size of eggs laid in the herring gull. *Condor* **78**: 481-492.

Partridge L & Harvey PH (1985) Costs of reproduction. *Nature* **316**: 20.

Partridge L & Harvey PH (1988) The ecological context of life history evolution. *Science* **241**: 1449-1455.

Patterson IJ (1965) Timing and spacing of broods in the black-headed gull, *Larus ridibundus. Ibis* **107**: 433-459.

Patterson IJ, Gilboa A & Tozer DJ (1982) Rearing other people's young: brood mixing in the shelduck *Tadorna tadorna. Anim. Behav.* **30**: 199-202.

Payne RB (1977) The ecology of brood parasitism in birds. *Ann. Rev. Ecol. Syst.* **8**: 1-28.

Pedersen HC & Steen JB (1985) Parental care and chick production in a fluctuating population of willow ptarmigan. *Ornis Scand.* **16**: 270-276.

Perrins CM (1966) Survival of young Manx shearwaters, *Puffinus puffinus*, in relation to their presumed date of hatching. *Ibis* **108**: 132-134.

Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* **112**: 242-255.

Perrins C (1977) The role of predation in the evolution of clutch size. *In: Stonehouse BM & Perrins CM (Eds) Evolutionary ecology. Univ. Park Pr., Baltimore:* pp 193-214.

Perrins C (1990) The illustrated encyclopaedia of birds. *Guild Publishing, London.*

Perrins CM & McCleery RH (1989) Laying dates and clutch-size in the great tit. *Wilson Bull.* **101**: 236-253.

Perrone M & Zaret TM (1979) Parental care patterns of fishes. *Amer. Natur.* **113**: 351-361.

Petrie M (1992a) Copulation frequency in birds: why do females copulate more than once with the same male? *Anim. Behav.* **44**: 790-792.

Petrie M (1992b) Peacocks with low mating success are more likely to suffer predation. *Anim. Behav.* **44**: 585-586.

Petrie M, Hall M, Halliday T, Budgey H & Pierpoint C (1992) Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once?. *Behav. Ecol. Sociobiol.* **31**: 349-358.

Petrie M, Halliday T & Sanders C (1991) Peahens prefer peacocks with elaborate trains. *Anim. Behav.* **41**: 323-332.

Petrie M & Hotchin N (unpub. manus.) Intra-specific brood parasitism in the moorhen (*Gallinula chloropus*): opportunistic parasites limited by host defences.

Petrie M & Møller AP (1991) Laying eggs in other's nests: intraspecific brood parasitism in birds. *Trends Ecol. Evol.* **6**: 315-320.

Petrinovich L (1974) Individual recognition of pup vocalization by northern elephant seal mothers. *Z. Tierpsychol.* **34**: 308-312.

Philipi T & Seger J (1989) Hedging one's evolutionary bets. *Trends Ecol. Evol.* **4**: 41-44.

Pianka ER (1976) Natural selection of optimal reproductive tactics. *Amer. Zool.* **16**: 775-784.

Pilters H (1954) Untersuchungen über angeborene Verhaltensweisen bei Tylopoden, unter besonderer Berücksichtigung der neuweltlichen Formen. *Z. Tierpsychol.* **11**: 213-303.

Pinxten R, Eens M & Verheyen RF (1991) Brood parasitism in European starlings: host and parasite adaptations. *Acta XX Con. Int. Orn.:* 1003-1011.

Plissner JH & Gowaty PA (1988) Evidence of reproductive error in adoption of nestling eastern bluebirds (*Sialia sialis*). *Auk* **105**: 275-278.

Power DM (Ed) (1989) Current Ornithology, Vol. 6. *Plenum Press, NY & London.*

Power HW, Kennedy ED, Romagnano LC, Lombardo MP, Hoffenberg AS, Stouffer PC & McGuire TR (1989) The parasitism insurance hypothesis: why starlings leave space for parasitic eggs.*Condor* **91**: 753-765.

Prevett JP & McInnes CD (1980) Family and other social groups in snow geese. *Wildl. Monogr.* **71**: 1-46.

Pugesek BH (1981) Increased reproductive effort with age in the California Gull (*Larus californicus*). *Science* **212**: 822-823.

Pulliam HR (1973) On the advantages of flocking. *J. Theor. Biol.* **38**: 419-422.

Pulliam HR & Caraco T (1984) Living in groups: is there an optimal group size? *In: Krebs JR & Davies NB (eds). Behavioural Ecology: an evolutionary approach. Blackwell, Oxford:* pp 122-147.

Rahn H & Ar A (1974) The avian egg: incubation time and water loss. *Condor* **76**: 147-152.

Ralls K (1976) Mammals in which females are larger than males. *Quart. Rev. Biol.* **31**: 245-276.

Ramsey AO (1951) Familial recognition in domestic birds. *Auk* **68**: 1-16.

Rands MRW, Ridley MW & Lelliott AD (1984) The social organisation of feral peafowl. *Anim. Behav.* **32**: 830-835.

Raveling D (1970) Dominance relationships and agonistic behaviour of Canada geese in winter. *Behaviour* **37**: 291-319.

Raveling DG (1981) Survival, experience and age in relation to breeding success of Canada geese. *J. Wildl. Manage.* **45**: 817-829.

Redondo T & Carranza J (1989) Offspring reproductive value and nest defense in the magpie (*Pica pica*). *Behav. Ecol. Sociobiol.* **25**: 369-378.

Regelmann K & Curio E (1983) Determinants of brood defence in the great tit. *Behav. Ecol. Sociobiol.* **13**: 131-145.

Reiter J & Le Boeuf BJ (1991) Life history consequences of variation in age at primiparity in northern elephant seals. *Behav. Ecol. Sociobiol.* **28**: 153-160.

Reyer HU & Westerterp K (1985) Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). *Behav. Ecol. Sociobiol.* **17**: 363-369.

Richdale LE (1957) A population study of penguins. *Oxford University Press, Oxford.*

Ricklefs RE (1969) An analysis of nestling mortality in birds. *Smithson Contr. Knowl. (Zool.)* **9**: 1-48.

Ricklefs RE (1974) Energetics of reproduction in birds. *In: Paynter RR (Ed) Avian energetics. Nuttal Ornithol. Club, Cambridge, MA:* pp 152-297.

Ricklefs RE (1975) The evolution of cooperative breeding in birds. *Ibis* **117**: 531-534.

Ricklefs RE (1977) On the evolution of reproductive strategies in birds: reproductive effort. *Amer. Natur.* **111**: 453-478.

Ricklefs RE (1980) Geographic variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* **97**: 38-49.

Ridley M (1978) Paternal care. *Anim. Behav.* **26**: 904-932.

Ridley M (1981) How the peacock got his tail. *New Scientist, 13th Aug:* pp 398-401.

Ridley MW (1983) The mating system of the pheasant *Phasianus colchicus. D.Phil. Thesis, Oxford University.*

Ridley MW, Lelliott AD & Rands MRW (1984) The courtship display of feral peafowl . *WPA Journal* **9**: 57-68.

Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.* **57**: 405-435.

Riedman ML & Le Boeuf BJ (1982) Mother-pup separation and adoption in northern elephant seals. *Behav. Ecol. Sociobiol.* **11**: 203-215.

Robbins CT (1983) Wildlife feeding and nutrition. *Academic Press, New York.*

Roberts BB (1940) The breeding behaviour of penguins with special reference to *Pygoscelis papua* (Forster). *Sci. Rep. Brit. Graham Land Exped. 1934-37* **3**: 195-254.

Robinson RH (1958) Use of nest boxes by wood ducks in the San Joaquin Valley, California. *Condor* **60**: 256-257.

Rockwell RF, Findlay CS & Cooke F (1987) Is there an optimal clutch size in snow geese? *Amer. Natur.* **130**: 839-863.

Rohwer FC (1984) Pattens of egg laying in prairie ducks. *Auk* **101**: 603-605.

Rohwer FC & Freeman S (1989) The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* **67**: 239-253.

Rood JP (1975) Population dynamics and food habits of the banded mongoose. *E. Afr. Wildl. J.* **13**: 89-112.

Rood JP (1978) Dwarf mongoose helpers at the den. *Z. Tierpsychol.* **48**: 277-287.

Rooth J (1965) The flamingoes on Bonaire. *Rivon Verhandeling No. 1.*

Rothstein SI (1971) Observation and experiment in the analysis of interactions between brood parasites and their hosts. *Amer. Natur.* **105**: 71-74.

Rothstein SI (1975a) Evolutionary rates and host defences against avian brood parasitism. *Amer. Natur.* **109**: 162-176.

Rothstein SI (1975b) An experimental and teleonomic investigation of avian brood parasitism. *Condor* **77**: 250-271.

Rothstein SI (1975c) Mechanisms of avian egg-recognition: do birds know their own eggs? *Anim. Behav.* **23**: 268-278.

Rothstein SI (1976a) Cowbird parasitism of the cedar waxwing and its evolutionary implications. *Auk* **93**: 498-509.

Rothstein SI (1976b) Experiments on defenses cedar waxwings use against cowbird parasitism. *Auk* **93**: 675-691.

Rothstein SI (1982) Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *Amer. Zool.* **22**: 547-560.

Royama T (1966) Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *Ibis* **108**: 313-347.

Royama T (1969) A model for the global variation of clutch size in birds. *Oikos* **20**: 562-567.

Rudge MR (1970) Mother and kid behaviour in feral goats (*Capra hircus* L.). *Z. Tierpsychol.* **27**: 687-692.

Rutgers A & Norris KA (Eds) (1970) Encyclopedia of aviculture, Volume 1. *Blandford Press, London.*

Ryder JP (1980) The influence of age on the breeding biology of colonial nesting seabirds. *In: Burger J, Olla BL & Winn HE (Eds) Behavior of marine mammals, Volume 4. Plenum Press, New York:* pp 153-168.

Sargent RC (1989) Allopaternal care in the fathead minnow *Pimephales promelas*: stepfathers discriminate against their adopted eggs. *Behav. Ecol. Sociobiol.* **25**: 379-385.

Sargent R & Gross MR (1986) Parental investment decision rules and the Concorde fallacy. *Behav. Ecol. Sociobiol.* **17**: 43-45.

Sargent R, Taylor PD & Gross MR (1987) Parental care and the evolution of egg size in fishes. *Amer. Natur.* **129**: 32-46.

Savard J-PL (1987) Causes and functions of brood amalgamation in Barrow's goldeneye and bufflehead. *Can. J. Zool.* **65**: 1548-1553.

Schaller GB (1964) Breeding behavior of the white pelican at Yellowstone lake, Wyoming. *Condor* **66**: 3-23.

Schaller GB (1972) The Serengeti lion: a study of predator-prey relations. *Univ. of Chicago Pr., Chicago.*

Schindler M & Lamprecht J (1987) Increase of parental effort with brood size in a nidifugous bird. *Auk* **104**: 688-693.

Schmutz JK, Robertson RJ & Cooke F (1982) Female sociality in the common eider duck during brood rearing. *Can. J. Zool.* **60**: 3326-3331.

Scott DM (1977) Cowbird parasitism on the gray catbird at London, Ontario. *Auk* **94**: 18-27.

Scott DK (1980) Functional aspects of prolonged parental care in Bewicks swans. *Anim. Behav.* **28**: 938-952.

Sedinger JS & Raveling DG (1990) Parental behavior of cackling Canada geese during brood rearing: division of labor within pairs. *Condor* **92**: 174-181

Selander RK (1965) On mating systems and sexual selection. *Amer. Natur.* **99**: 129-141.

Semel B, Sherman PW & Byers SM (1988) Effects of brood parasitism and nest-box placement on wood duck breeding ecology. *Condor* **90**: 920-930.

Shaller GB (1964) Notes on the behaviour of the peafowl. *Newspaper for birdwatchers (Bombay)* **4**: 1-3.

Sharma IK (1969) Habitat et compartement du paon (*Pavo cristatus*). *Alauda* **37**: 219-223.

Sharma IK (1972) Étude écologique de la reproduction du paon *Pavo cristatus*. *Alauda* **40**: 378-384.

Sharma IK (1974) Ecological studies of the plumes of the peacock (*Pavo cristatus*). *Condor* **76**: 344-346.

Sharma IK (1978) Social and sexual behaviours of the Peafowl - *Pavo cristatus*. *Environmental Awareness* **1**: 169-171.

Sherley GH (1990a) Cooperative breeding in riflemen (*Acanthisitta chloris*): benefits to parents, offspring and helpers. *Behaviour* **112**: 1-22.

Sherley G (1990b) Relative parental effort during incubation in riflemen (*Acanthasitta chloris*). *N.Z. J. Zool.* **17**: 289-294.

Sherman PW (1977) Nepotism and the evolution of alarm calls. *Science* **197**: 1246-1253.

Shine R (1978) Propagule size and parental care: the "Safe Harbor" hypothesis. *J. Theoret. Biol.* **75**: 417-424.

Shine R (1989) Alternative models for the evolution of offspring size. *Amer. Natur.* **134**: 311-317.

Shugart GW (1977) The development of chick recognition by adult caspian terns. *Proc. Colonial Waterbird Group* **1**: 110-117.

Sibly RM (1983) Optimal group size is unstable. *Anim. Behav.* **31**: 3

Sibly RM & Calow P (1986) Physiological ecology of animals: an evolutionary approach. *Blackwell Scientific Publications.*

Siegel S (1956) Non-parametric statistics for the behavioural sciences. *McGraw-Hill, New York.*

Silver R (1985) Prolactin and parenting in the pigeon family. *J. Exp. Zool.* **232**: 617-625.

Simmons KEL (1955) The nature of the predator reactions of waders towards humans, with special reference to the role of the aggressive-, escape-, and brooding-drives. *Behaviour* **8**: 130-173.

Skutch AF (1957) The parental strategems of birds. *Ibis* **97**: 118-142.

Skutch AF (1976) Parent birds and their young. *Univ. of Texas Pr., Austin, Texas.*

Sladen WJ (1958) The Pygoscelid penguins. *C.I.D.S. Sci. Reports: No. 17.*

Slagsvold T (1982) Sex, size and natural selection in the hooded crow *Corvus corone cornix*. *Ornis Scand.* **13**: 165-175.

Slagsvold T (1984) Clutch size variation in birds in relation to nest predation - on the cost of reproduction. *J. Anim. Ecol.* **53**: 945-953.

Slagsvold T, Sandvik J, Rofstad G, Lorentsen O & Husby M (1984) On the adaptive value of intraclutch egg-size variation in birds. *Auk* **101**: 685-697.

Smith CC & Fretwell SD (1974) The optimal balance between size and number of offspring. *Amer. Natur.* **108**: 499-506.

Smith HG (1989) Larger clutches take longer to incubate. *Ornis Scand.* **20**: 156-158.

Smith JNM (1990) Summary. *In: Stacey PB & Koenig WD (Eds) Cooperative breeding in birds: long-term studies of ecology and behaviour. Cambridge Univ. Pr.* pp 593-611.

Snow BK (1963) The behaviour of the shag. *British Birds* **56**: 77-103, 164-186.

Sonerud GA (1988) To distract display or not - grouse hens and foxes. *Oikos* **51**: 233-237.

Spellerberg IF (1971) Breeding behaviour of the McCormick skua *Catharacta maccormicki* in Antarctica. *Ardea* **59**: 189-230.

Spencer-Booth Y (1970) The relationship between mammalian young and conspecifics other than mothers and peers: a review. *In: Lehrman DS, Hinde RA & Shaw E (Eds) Advances in the study of behavior, Vol. 3. Academic Pr.,* pp 120-180.

Sprunt A iv (1988) The greater flamingo. *In: Chandler WJ (Ed) Audobon Wildlife Report 1988/89:* pp 553-564.

Stamps JA (1990) When should avian parents differentially provision sons and daughters? *Amer. Natur.* **135**: 671-685.

Stearns SC (1976) Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* **51**: 3-48.

Stearns SC (1992) The evolution of life histories. *Oxford University Press, Oxford.*

Steele DH (1977) Correlation between egg size and development period. *Amer. Natur.* **111**: 371-372.

Stokes DL & Boersma PD (1991) Effects of substrate on the distribution of Magellanic penguin (*Spheniscus magellanicus*) burrows. *Auk* **108**: 923-933.

Stokland JN & Amundsen T (1988) Initial size hierarchy in broods of the shag: significance of egg size and hatching asynchrony. *Auk* **105**: 308-315.

Stonehouse B (1953) The emperor penguin *Aptenodytes forsteri* (Gray). I. Breeding behaviour and development. *F.I.D.S. Sci. Reports: No. 6.*

Stonehouse B (1960) The king penguin *Aptenodytes patagonica* of South Georgia. I. Breeding behaviour and development. *F.I.D.S. Sci. Reports: No. 23.*

Sutherland WJ (1985) Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Anim. Behav.* **33**: 1349-1352.

Swynnerton CFM (1918) Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. *Ibis:* 127-154.

Tavolga MC & Essapian FS (1957) Behavior of the bottle-nose dolphin (*Tursiops truncatus*): mating, pregnancy, parturition, and mother-infant behavior. *Zoologica* **42**: Nov-31.

Thaker JP (1963) Peacock: the national bird of India. *Pavo* **1**: 1-18.

Thornhill R & Alcock J (1983) The evolution of insect mating systems. *Harvard Univ. Pr., Cambridge, MA.*

Thornhill R (1976) Sexual selection and paternal investment in insects. *Amer. Natur.* **110**: 153-163.

Thornhill R (1989) Nest defense by red junglefowl (*Gallus gallus spadiceus*) hens: the roles of renesting potential, parental experience and brood reproductive value. *Ethology* **83**: 31-42.

Tinbergen N (1953) The herring gull's world. *Collins, London.*

Trivers RL (1971) The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**: 35-37.

Trivers RL (1972) Parental investment and sexual selection. *In: Campbell B (Ed): Sexual Selection and the Descent of Man, 1871-1971. Aldine, Chicago:* pp 136-179.

Trivers RL (1974) Parent-offspring conflict. *Amer. Zool.* **14**: 249-264.

Trivers RL & Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**: 90-92.

Turcotte Y & Bédard J (1989) Shared parental investment, parent-offspring conflict and brood size in greater snow geese. *Anim. Behav.* **38**: 703-706.

van Lawick H & van Lawick-Goodall J (1971) Innocent killers. *Houghton Mifflin, Boston.*

Vance RR (1973a) On reproductive strategy in marine benthic invertebrates. *Amer. Natur.* **107**: 339-352.

Vance RR (1973b) More on reproductive strategies in marine benthic invertebrates. *Amer. Natur.* **107**: 353-361.

Vehrencamp SL (1977) Relative fecundity and parental effort in communally nesting anis *Crotophoga sulcirostris. Science* **197**: 403-405.

Vestjens WJM (1977) Breeding behaviour and ecology of the Australian pelican, *Pelecanus conspicillatus*, in New South Wales. *Austr. Wildl. Res.* **4**: 37-58.

Wagner FH, Besadny CD & Kabat C (1965) Population ecology and management of Wisconsin pheasants. *Wisconsin Conservation Bulletin* **35**: 1-168.

Waldman B (1988) The ecology of kin recognition. *Ann. Rev. Ecol. Syst.* **19**: 543-571.

Waldman B, Frumhof PC & Sherman PW (1988) Problems of kin recognition. *Trends Ecol. Evol.* **3**: 8-13.

Walters JR (1982) Parental behavior in lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. *Evolution* **36**: 1030-1040.

Warhurst RA, Bookhout TA (1983) Effect of gang brooding on survival of Canada goose goslings. *J. Wildl. Manage.* **47**: 1119-1124.

Warner RE (1984) Effects of changing agriculture on ring-necked pheasant brood movements in Illinois. *J. Wildl. Mgmt.* **48**: 1014-1018.

Warner RR (1984) Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. *Evolution* **38**: 148-162.

Weller MW (1959) Parasitic egg laying in the redhead and other North American Anatidae. *Ecol. Monogr.* **29**: 333-365.

Welty JC & Baptista L (1988) The life of birds (4th edition) *Saunders Coll. Publ.*

Wenke DJ (1989) Sexing pheasant chicks. *WPA News* **25**: 38.

West Eberhard MJW (1975) The evolution of social behaviour by kin selection. *Quart. Rev. Biol.* **50**: 1-33.

Westcott DA & Cockburn A (1988) Flock size and vigilance in parrots. *Aust. J. Zool.* **36**: 335-349

Western D & Ssemakula J (1982) Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* **54**: 281-290.

Westmoreland D (1989) Offspring age and nest defence in mourning doves: a test of two hypotheses. *Anim. Behav.* **38**: 1062-1066.

Wiklund CG (1990a) The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Anim. Behav.* **40**: 244-253.

Wiklund CG (1990b) Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. *Behav. Ecol. Sociobiol.* **26**: 217-223.

Wiley RH (1974) Evolution of social organisation and life-history patterns among grouse. *Quart. Rev. Biol.* **49**: 201-227.

Williams GC (1966a) Adaptation and natural selection. *Princeton Univ. Pr., Princeton.*

Williams GC (1966b) Natural selection, the costs of reproduction and a refinement of Lack's principle. *Amer. Natur.* **100**: 687-690.

Williams GC (1975) Sex and evolution. *Princeton Univ. Pr., Princeton, N.J.*

Williams TD (1994) Adoption in a precocial species, the lesser snow goose: intergenerational conflict, altruism or a mutually beneficial strategy? *Anim. Behav.* **47**: 101-107.

Williams M (1974) Creching behaviour of the shelduck *Tadorna tadorna* L. *Ornis Scandinavica* **5**: 131-143.

Willson MF & Pianka EF (1963) Sexual selection, sex ratio and mating system. *Amer. Natur.* **97**: 405-407.

Wilson EO (1975) Sociobiology. *Belknap Press, Harvard.*

Windt W & Curio E (1986) Clutch defence in great tit (*Parus major*) pairs and the Concorde fallacy. *Ethology* **72**: 236-242.

Winkler DW (1987) A general model for parental care. *Amer. Natur.* **130**: 526-543.

Winkler DW & Wallin (1987) Offspring size and number: a life history model linking effort per offspring and total effort. *Amer. Natur.* **129**: 708-720.

Winkler DW & Walters JR (1983) The determination of clutch size in precocial birds. *In: Johnston RF (Ed): Current Ornithology, Volume 1. Plenum Press, NY & London:* pp 33-68.

Wittenberger JF (1979) The evolution of mating systems in birds and mammals. *In: Master P & Vandenburgh J (Eds) Handbook of Behavioral Neurobiology: Social behavior and communication. Plenum Pr., NY:* pp 271-349.

Wooldridge FL (1969) Behavior of the Abyssinian colobus monkey, *Colobus guereza*, in captivity. *M.A. Thesis, Univ. Florida, Gainsville.*

Woolfenden GE (1975) Florida scrub jay helpers at the nest. *Auk* **92**: 1-15.

Woolfenden GE (1976) Cooperative breeding in American birds. *Acta XVI Int. Ornith. Congr:* pp 674-684.

Woolfenden GE & Fitzpatrick JW (1984) The Florida scrub jay: demography of a cooperative-breeding bird. *Monogr. Popul. Biol.* **20**.

Wootton RJ (1979) Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. Lond.* **44**: 133-159.

Wootton RJ (1984) A functional biology of sticklebacks. *Croom Helm, London.*

Yamauchi A (1993) Theory of intraspecific nest parasitism in birds. *Anim. Behav.* **46**: 335-345.

Yom-Tov Y (1976) Recognition of eggs and young by the carrion crow (*Corvus corone*). *Behaviour* **59**: 247-251.

Yom-Tov Y (1980) Intraspecific nest parasitism in birds. *Biol. Rev.* **55**: 93-108.

Yom-Tov Y & Hilborn R (1981) Energetic constraints on clutch size and time of breeding in temperate zone passerines. *Oecologia* **48**: 234-243.

Zahavi A (1979) Parasitism and nest predation in parasitic cuckoos. *Amer. Natur.* **113**: 157-159.